CANADIAN JOURNAL OF RESEARCH

VOLUME 15 OCTOBER, 1937 NUMBER 10

CONTENTS

SEC. C.—BOTANICAL SCIENCES

Page

Chemical Weed Killers. IV. Relative Toxicities and Loci of Absorption of Selected Chemicals Applied to Perennials —*W. H. Cook* - - - - - - - - - - - - - 451

Agricultural Meteorology: Some Characteristics of Air Temperature in Alberta and Saskatchewan—*J. W. Hopkins* - 461

SEC. D.—ZOOLOGICAL SCIENCES

Larval and Adult Stages of British Columbia Anomura —*Josephine F. L. Hart* - - - - - - - - - - 179

NATIONAL RESEARCH COUNCIL
OTTAWA, CANADA

Publications and Subscriptions

The Canadian Journal of Research is issued monthly in four sections, as follows:

A. Physical Sciences
B. Chemical Sciences
C. Botanical Sciences
D. Zoological Sciences

For the present, Sections A and B are issued under a single cover, as also are Sections C and D, with separate pagination of the four sections, to permit separate binding, if desired.

Subscription rates, postage paid to any part of the world, are as follows:

	Annual	*Single Copy*
A and B	$ 2.50	$ 0.50
C and D	2.50	0.50
Four sections, complete	4.00	—

The Canadian Journal of Research is published by the National Research Council of Canada under authority of the Chairman of the Committee of the Privy Council on Scientific and Industrial Research. All correspondence should be addressed:

National Research Council, Ottawa, Canada.

Reprinted in entirety by photo-offset from the original issue.

1984

Canadian Journal of Research

Issued by THE NATIONAL RESEARCH COUNCIL OF CANADA

VOL. 15, SEC. C. OCTOBER, 1937 NUMBER 10

CHEMICAL WEED-KILLERS

IV. RELATIVE TOXICITIES AND LOCI OF ABSORPTION OF SELECTED CHEMICALS APPLIED TO PERENNIALS[1]

BY W. H. COOK[2]

Abstract

Twelve chemicals previously found to be highly toxic to annual weeds were applied to a perennial weed in three different ways, *viz.*, to the foliage only, to the soil only, and to both the soil and foliage. The chlorate ion was found to be most toxic, but sodium selenite, ammonium thiocyanate, sodium dichromate, and sodium arsenite were all reasonably effective at higher dosages. None of the other chemicals caused any significant, permanent reduction in growth at the dosages used. The permanent effect of a treatment appears to be due almost entirely to the action of the chemical in the soil, and the ineffectiveness of certain chemicals can be attributed to their rapid detoxication by the soil. Although all the chemicals exert a temporary, and in some cases, a slight permanent effect, when applied to the foliage only, this method of application is generally ineffective owing to the inability of the leaves and stems to retain or absorb a lethal dosage.

Introduction

This investigation was undertaken to obtain further information on the relative toxicities of certain chemicals to perennials, and also to determine whether these substances, when applied as a spray, entered the plant through the foliage, the roots, or through both these loci. The chemicals were selected from those previously found to be most toxic to annuals (2), but a number of them were not included since they had been found to be ineffective in field tests on perennials (4).

Materials and Methods

For the most part these experiments were made in an ordinary greenhouse in the same way as the previous tests on annuals (2). Perennial sow thistle, *Sonchus arvensis* L., was the only weed used. The plants were grown from root cuttings planted in the experimental crocks, and allowed to develop for a year before the various treatments were made. During this period the plants were cut back to prevent flowering, and fertilized several times. Before treatment all the weeds had a well developed root system which extended throughout the soil in the crock. The number of stems in each crock at the time of treatment varied from 2 to 5, the majority of plants having 4; the height also varied from 3 to 9 in. but a height of 6 to 7 in. was usual. The

[1] *Manuscript received August 12, 1937.*
Contribution from the Division of Biology and Agriculture, National Research Laboratories, Ottawa. Issued as paper No. 17 of the Associate Committee on Weed Control.
[2] *Biologist, National Research Laboratories, Ottawa.*

actual amount of foliage per crock was much more uniform than either the number of plants per crock or their height, because a reduction in number of plants per crock was compensated for by increased size of individual plants. To obviate any possible systematic error due to variable size, the crocks were distributed at random among dosages, treatments, and chemicals, and all phases of the experiments made concurrently.

Four dosages of each chemical were applied in all treatments, namely, 260, 520, 1050 and 2100 lb. per acre. The concentration of the solution sprayed on the plants was varied so that all these doses were applied in a volume of solution equivalent to 1050 gal. per acre. This procedure was followed so that the quantity of chemical retained by the foliage would be approximately proportional to the total dosage applied (3). This was important since three modes of application, *i.e.*, to the foliage only, to the soil only, and to both loci, were to be used. Ten of the 12 chemicals studied were applied in this way, namely, chloric acid, sodium chlorate, arsenic pentoxide, sodium arsenite, ammonium thiocyanate, sodium cyanide, copper nitrate, sodium selenite, sodium dichromate and phenol. Sodium sulphide and formic acid were applied only by the regular spray technique, *i.e.*, to both loci at once, to determine their relative toxicity.

The application of the toxic solution to the foliage only was accomplished by covering the surface of the soil with a coating of paraffin wax before spraying by the usual procedure. The amount of solution that drained to this wax covering was then collected and the quantity retained by the leaves estimated from the difference between the applied and recovered volumes. The retained volume varied with the size of the plants from $\frac{1}{8}$ to $\frac{1}{4}$ of the volume applied. Any chemical remaining on the wax covering was washed off two days later and the wax removed. Applications to the soil only were made with a pipette, the solution being well distributed over the surface. The usual spraying procedure was used to apply the toxic solution to both the foliage and soil. Two types of controls were used, the original plants being allowed to grow in one set, while in the other they were cut back to the soil level at the time of treatment in order to produce conditions comparable with chemical applications which affect the foliage only. Each treatment of whatever kind was made in duplicate, with an additional number of controls.

The plants were treated in the middle of May. Periodic observations were made thereafter to determine the mortality of the original foliage and the time required for new plants to develop. The final observations were made four months after treatment, when the number and wet weight of the surviving plants (stems and leaves) were determined. Dead stems and tissue were removed before weighing the living material. This could be done quite accurately in these tests, since the elapsed time from treatment and death of the original stems was of sufficient duration to permit precise distinctions. One week later the crocks were seeded to wheat to determine whether any residual toxic effect persisted in the soil.

Results

Observations Following Treatment

Of the observations taken between the time of treatment and the final quantitative determinations, the times required for the death of the leaves on the original plants, and for the development of new plants, appear to be the most valuable. These results are summarized in Table I, the chemicals being arranged in groups in order of toxicity. While the lowest dosages were generally least effective (see Table II) and acted more slowly than the higher dosages, the rates of action were not sufficiently different to justify detailed consideration. Some idea of the variability can be gained from the range of values reported in Table I. It was observed that, if a long period was required

TABLE I

Days from treatment until death of leaves and appearance of new plants

Chemical	Application to foliage only		Application to soil only		Application to both foliage and soil	
	Days for death of leaves	Days for appearance of new plants	Days for death of leaves	Days for appearance of new plants	Days for death of leaves	Days for appearance of new plants
Sodium chlorate	30–40*	10	21-60	20–69	32–64	65–75
Chloric acid	2–3	5–6	25–50	60†	2–3	3–9
Sodium selenite	3	7–10	90*	30–90†	3	5–10†
Ammonium thiocyanate	3	7–10	7–28	7–28	4–5	5–10†
Sodium dichromate	2	7	10–50	15–63†	2-4	7–40†
Sodium arsenite	3–4	10–12	6–10*	14–30	4	4–20
Sodium cyanide	3	7–14	7–10*	10–50	3	7–10
Arsenic pentoxide	3	7–14	No effect beyond wilting		3	3–14
Copper nitrate	2	6–8	No effect beyond slight wilting		2	6–8
Phenol	2–4*	6–8	No effect beyond slight wilting		2–4*	8–30
Sodium sulphide	–	–	–	–	3*	14–30
Formic acid	–	–	–	–	1–2	2–3

* *Leaves and stems revived at low doses.*
† *No new growth at high doses.*

for the death of the original foliage, the development of new plants was also slower, indicating that the plant tends to maintain the original foliage at the expense of new plant development. Quantitative information was obtained only from the final determinations, which will now be considered.

Final Determinations

The number and weight, of plants in each crock four months after treatment were the two criteria used to estimate the efficacy of the treatment. These results are given in Table II. Before discussing them, the relative value of the two criteria must be considered, for, although they generally

agree, there are some cases of divergence. Mortality is the criterion commonly used for measuring toxicity, and comparisons of the number of plants in the treated and untreated crocks probably give the best estimate of this quantity. At the same time it must be recognized that this is not a per-

TABLE II

EFFECT OF CHEMICAL AND METHOD OF APPLICATION ON NUMBER AND GREEN WEIGHT OF LIVING STEMS AND LEAVES

Chemical and dosage, lb. per acre	No. of plants per crock — Mean of duplicates			Wet wt. of plants per crock — Mean of duplicates		
	Application to foliage only	Application to soil only	Application to foliage and soil	Application to foliage only, gm.	Application to soil only, gm.	Application to foliage and soil, gm.
Sodium chlorate						
260	11.5(1) *	1 5	1	86.5(1)	15.0	7.0
520	7.5	0	0	85.0(1)	0	0
1050	10.0(1)	0	0	55.5	0	0
2100	1.0(2)	0	0	12.0(2?)	0	0
Chloric acid						
260	13.5(1)	2.0	5.0	55.5	13.5	43.0
520	2.0(2)	0.5	0	39.0	1.5	0
1050–2100	0	0	0	0	0	0
Sodium selenite						
260	13.5(1)	5.0	9.0	98.5	76.0	77.0(1)
520	2.5(2)	2.5	3.5	96.0	42.0	76.5
1050	7.0	3.5	0.5	66.5	25.0	14.5(2)
2100	5.0	0	0	71.5	0	0
Ammonium thiocyanate						
260	8.0	6.0	9.5	48.0	52.5	107.0(1)
520	13.0(1)	11.5(1)	8.0	104.0(1)	73.5(1)	58
1050	12.5	0.5(2)	1.0	108.5(1)	5.0(2)	27 (2)
2100	2.0(2)	0	0	38.5(2)	0	0
Sodium dichromate						
260	13.0(1)	9.0	13.5(1)	71.5	62.5	82.5
520	11.5	1.0	6.0	100.0(1)	37.0	81.0
1050	10.0	6.0	0.5(2)	80.0	89.5	32.0
2100	4.0(2)	0	0	32.5(2)	0	0
Sodium arsenite						
260	12.0	8.5	6.0	76.5	75.5(1)	97.5(1)
520	13.5	6.5	2.0	61.5	85.0(1)	61.5
1050	11.0	2.5	0	85.0	58.5	0
2100	12.0	0.5	0.5	46.0	1.5(2)	12.5(2)
Sodium cyanide						
260	19.5(1)	12.5(1)	13.0(1)	83.5	89.0	85.0
520	6.5(2)	8.5	12.5(1)	77.5	82.0	77.0
1050	12.0	5.0	5.0	97.5	59.5	61.0
2100	16.5	1.5(2)	2.5 (2)	77.5	33.5	25.5
Arsenic pentoxide						
Mean of all 4 doses	3.4	8.0	3.6	70.0	95.4†	42.5†

* *Quantities marked (1) are significantly different from quantities marked (2) for same chemical and mode of application.*

† *These two significantly different.*

TABLE II—*Concluded*

EFFECT OF CHEMICAL AND METHOD OF APPLICATION ON NUMBER AND GREEN WEIGHT OF LIVING STEMS AND LEAVES—*Concluded*

Chemical and dosage, lb. per acre	No. of plants per crock. Mean of duplicates			Wet wt. of plants per crock. Mean of duplicates		
	Application to foliage only	Application to soil only	Application to foliage and soil	Application to foliage only, gm.	Application to soil only, gm.	Application to foliage and soil, gm.
Copper nitrate						
Mean of all 4 doses	12.4	18.8	13.6	77.0	92.4	88.9
Phenol						
Mean of all 4 doses	11.2	12.6	13.4	80.2	77.6	91.4
Sodium sulphide						
Mean of all 4 doses			12.6			77.6
Formic acid						
Mean of all 4 doses			10.6			93.8
Controls						
Cut back		18.7(1)				
Allowed to grow		8.0(2)				
				77.6 (Mean of both types of controls as not significantly different.)		

* *Quantities marked (1) are significantly different from quantities marked (2) for same chemical and mode of application.*

centage mortality comparable with that obtained with organisms in which the final effect can be observed within a short period after treatment. During the period allowed between treatment and the final count, the number of plants in the cut and uncut controls increased from an average of 3.6 plants per crock to 18.7 and 8.0 respectively. This shows that growth during this period introduces one complication. In the treated crocks this complication becomes more serious; a given poison might cause high mortality in the original plants, including the roots, but if the chemical is detoxicated in the soil, a small amount of living root material might re-establish the original number of plants before the final observations are made. This behavior is believed to account for the high variability observed between duplicates in these experiments. Finally, any estimate of the number of plants of a perennial weed is really an estimate of the number of stems, many of which may come from a common root. These may correctly be termed plants if they can exist separately, but they might not behave as such toward an applied chemical.

From a practical standpoint the size and number of weeds per unit area, and their rate of re-establishment, determine their competitive influence on economic crops. The number alone is of little value, for if only a few plants survive they may be large, and *vice versa*. It appears, therefore, that a

practical measure of efficacy, such as the weight of weed material, is the best criterion of toxicity to use, until more is known about the dosage-mortality relations of poisons and perennial weeds.

An initial study of the weight of the plants was made by computing the averages obtained from all crocks at all dosages for each chemical and method of application, and studying the results statistically. Taking a 5% level of significance, it was found that the chemicals could be classified into four distinct groups which differed significantly from one another. Sodium chlorate and chloric acid caused the greatest reduction in weight and constituted the first group; sodium selenite, ammonium thiocyanate, sodium dichromate and sodium arsenite the second; sodium cyanide and arsenic pentoxide the third, which did not differ significantly from the controls; and sodium sulphide, copper nitrate, phenol and formic acid the last group, in which the weight of plant material was significantly greater than in the controls, suggesting direct or indirect stimulation or nutritive effects. Application of the chemical to the foliage or soil only, or to both loci, gave essentially the same grouping.

Since all the chemicals were applied at the same dosages, such an analysis is useful for comparative purposes, but it gives no information as to the effect of different dosages. These more detailed results are given in Table II, where the chemicals are again arranged in order of decreasing toxicity, although the differences are significant only between the groups indicated. Sodium chlorate appears first and, although it did not differ significantly from chloric acid, the figures suggest that it is slightly less toxic than the latter. It must be remembered, however, that, on the basis of chlorate ion, the applied dosage of sodium chlorate was only 78% of that applied as chloric acid.

The first six chemicals caused complete mortality at one or more of the higher dosages. The certainly lethal dose gives an estimate of their relative toxicities, but the data do not permit evaluation of the extent to which these lethal dosages may be in error. Where a given treatment did not give a complete kill, but the number or weight of plants differed significantly between doses, the results are given, and the quantities that differ significantly are indicated. Owing to the large variability between duplicates, only relatively large differences were significant. Where the weights of the plants did not differ significantly, and the significant differences between the number of plants did not appear to be related to the dosage, the mean values at all dosages are the only figures reported. Actually the significant differences between the numbers of plants in crocks receiving different dosages of copper nitrate suggested stimulation with increasing dosages, while phenol appeared to be the most effective as a poison at intermediate doses.

It is evident that the first six chemicals were about equally effective whether applied to the soil only, or to the foliage and soil, but were comparatively ineffective when applied to the foliage only. The significant differences between dosages applied only to the leaves indicate that, with the possible exception of sodium arsenite, all the chemicals can bring about a permanent reduction

in growth through the foliage but are comparatively ineffective owing to the inability of the leaves to retain or absorb a lethal quantity. The efficacy of sodium chlorate applied to the leaves must also be questioned, since a slight residual effect, discussed in the next section, was evident in one of the crocks, indicating that some of the chemical might have entered the soil through the wax. It should also be noted that chloric acid was comparatively more effective than the other chemicals when applied to the foliage only.

The remaining chemicals produced no evidence of a permanent effect and consequently showed little difference between the three methods of application. Arsenic pentoxide, applied to the soil only, gave significantly higher plant weights than applications to foliage and soil. Neither treatment differed significantly from the controls, so that the above results must be attributed to stimulation following applications to the soil, and a slight toxic action when applied to both foliage and soil.

Residual Effect in Soil

After the final determinations were made on the weeds, the crocks were seeded with wheat to determine whether there remained a residual toxic effect in the soil. The final observations on these plants were made 45 days after seeding. In general, only crocks that had received the two highest dosages were used. Crocks representing each method of application of sodium chlorate and chloric acid were tested, since these chemicals were effective when applied by all three methods. Crocks, in which the other chemicals had been applied to the foliage only, were excluded, since such treatments were ineffective. Crocks treated by all methods with copper nitrate, phenol, sodium sulphide, and formic acid were excluded for similar reasons.

The results will not be presented in detail, but are summarized below:—

Sodium chlorate. Applications to soil showed definite evidence of residual chemical, the plants being small and weak. Applications to the foliage only left no residual effect, except in one crock that received the maximum dosage, in which the plants were somewhat smaller than in the control crocks.

Chloric Acid. Applications to soil left a residual effect that increased with applied dosage. No effect was evident following applications to foliage only.

Sodium selenite. Plants died within three weeks in crocks that had received the two highest dosages applied to the soil. Applications to foliage and soil also left a marked residual toxic effect, which did not result, however, in complete mortality.

Sodium arsenite. Only slight evidence of residual chemical showed in crocks that had received the two highest dosages applied to the soil; similar dosages applied to both foliage and soil had no apparent residual toxic effect.

Arsenic pentoxide. Only slight evidence appeared of residual chemical following applications of maximum dosage to foliage and soil.

Ammonium thiocyanate, *sodium dichromate*, and *sodium cyanide*. No evidence was found of any residual chemical in the soil.

This summary shows that the chlorate and selenite ions have a decided residual effect. The fact that sodium selenite has less effect than the chlorates on the growth of thistles, and an equal or greater effect on the growth of wheat planted subsequently, must be attributed to a difference in the susceptibility of sow thistle and wheat to this chemical. A difference in the susceptibility of these two plants to arsenicals would also explain the residual toxic effects observed with wheat in crocks that had previously supported considerable growth of thistles. Substances that killed the thistles but showed no residual effects must have been detoxicated before the wheat was planted, at least to a point below that at which wheat was affected.

Discussion and Conclusions

All the chemicals tested, with the exception of sodium chlorate, killed the leaves of the plants within a few days after treatment when applied directly to the foliage; four months later, however, reduction of the weed growth was apparent for only 6 of the 12 chemicals used. This shows that the mere destruction of the foliage is no indication of the efficacy of a herbicide. Of the six effective chemicals, sodium chlorate and chloric acid were significantly more toxic than sodium selenite, ammonium thiocyanate, sodium dichromate and sodium arsenite. The certainly lethal dose of the last chemical might be higher than the maximum dose employed, but it reduced growth to such an extent that, on the basis of weight, its toxicity did not differ significantly from that of the other chemicals in the second group.

In general, the toxic chemicals were equally effective whether applied to the soil only or to the foliage and soil, but were comparatively ineffective when applied to the foliage only. The latter result is attributable to the inability of the aerial parts to retain or absorb more than a small proportion of the applied dosage. Chloric acid was the only exception to this rule, for although applications to the foliage only were generally least deadly, this method of application proved to be relatively more effective with this chemical than with the other chemicals tested. These results show that the observed reduction in the number and size of perennial plants, following the application of a herbicide as a spray, is due mainly to the action of the chemical in the soil, rather than to its direct effect on the leaves.

All the chemicals used in these experiments were inherently quite toxic to plants as judged from their effect on annual weeds (2) and on the foliage of perennials. Since the mortality of perennials is due, however, almost entirely to the presence of the poison in the soil, it follows that the detoxicating effect of the soil, rather than the inherent toxicity of the chemical, is the factor limiting the efficacy of certain substances. The permanent effect of chemical sprays will depend, therefore, on the relative rates of poisoning and detoxication and, if the latter reaction is rapid compared with the former, the treat-

ment will be ineffective. Some estimate of the rate of poisoning can be obtained from the time required to kill the leaves, following applications to the soil only. This period varied from 10 to 60 days, and, in general, the slowest acting chemicals proved to be most effective. Certain chemicals did not kill any of the leaves, when applied to the soil, indicating that these substances were detoxicated within a relatively short period. It appears, from these considerations, that the observed variability in the relative toxicity of different chemicals to perennials is due mainly to variable detoxication by the soil rather than to variable susceptibility of the plants grown under different conditions. A herbicide which is consistently effective under all conditions will, therefore, be one which is not readily detoxicated by any soil, and will remain effective for a period of 60 to 90 days until all plant roots are dead. The efficacy of chlorates can be explained on this basis, since they are apparently not detoxicated as rapidly by different soils as certain other compounds used as herbicides (1, 5). Arsenicals, although they are inherently quite toxic, are apparently susceptible to detoxication in certain soils, at least to a level where they are ineffective against perennials. Thus arsenic pentoxide appeared to be quite effective in field tests (4) but was quite useless in these experiments.

If the efficacy of a given perennial herbicide is to be rendered independent of the soil, some consideration should be given to the possibility of poisoning the plants through the leaves. Furthermore, since the efficacy of chemicals acting through the soil is at least reduced by dilution, if not by detoxication, it seems probable that the certainly lethal dose of a given chemical would be lower if it could be made to act through the leaves rather than through the soil. The comparative ineffectiveness of applications to the foliage only in these experiments can be attributed entirely to the inability of the leaves and stems to retain or absorb a lethal dosage, since in no case was more than $\frac{1}{4}$ of the applied dosage retained by the leaves and stems. At the same time the number and weight of plants was reduced significantly in several cases as the dosage, *i.e.*, concentration, applied to the foliage only, was increased. This suggests that the chemical can act through the leaves and might be effective if retained and absorbed by the foliage in sufficient quantity. If this is so, the quantity retained could be increased by increasing the concentration of the spray solution (3) within the limits of the solubility of the chemical. The results obtained with chloric acid suggest that an acid condition favors absorption.

In conclusion it is worth noting again that with the composition of the solutions commonly applied to perennials as herbicides, the permanent lethal effect observed comes almost entirely from the action of the chemical in the soil. Under these conditions any system of sprinkling or distributing the solution over the soil area should prove effective. For annual weeds, however, where the comparatively much smaller dosages required act almost entirely on the foliage, a good distribution of the solution over the leaves is essential.

Acknowledgments

The author wishes to thank Mr. G. N. Seed and Mr. A. E. Chadderton, Laboratory Assistants, National Research Laboratories, for technical assistance during the course of this investigation.

References

1. Bowser, W. E. and Newton, J. D. Can. J. Research, 8 : 73-100. 1933.
2. Cook, W. H. Can. J. Research, C, 15 : 299-323. 1937.
3. Cook, W. H. Can. J. Research, C, 15 : 380-390. 1937.
4. Cook, W. H., Pavlychenko, T. K., Manson, J. M. and Garrow, P. Can. J. Research, C, 15 : 442-449. 1937.
5. Newton, J. D. and Paul, A. D. Can. J. Research, C. 13 : 101-114. 1935.

AGRICULTURAL METEOROLOGY: SOME CHARACTERISTICS OF AIR TEMPERATURE IN ALBERTA AND SASKATCHEWAN[1]

By J. W. Hopkins[2]

Abstract

A five-year moving average of mean temperature for the period April 1 to August 31 has a range of variation of about 4° F. over the years 1893–1933 at Edmonton and Calgary (central and southern Alberta), and Battleford and Swift Current (central and southern Saskatchewan). The general trend over the 41 years is slightly upward at the last three stations; there are also shorter irregular cycles of above- and below-average values of both mean temperature and mean daily range at all four stations. Short-term fluctuations of the former are most pronounced in April and May; those of the latter are equally in evidence in all five months. The annual averages of daily mean temperature (April 1–August 31) tend at all four stations to fall more frequently above than below the general average for the 41 years. Annual variation in monthly mean temperature is greatest in April and least in July, but the mean daily range is as variable for the summer as for the spring months. There is a fairly close correlation between the annual variations in mean monthly temperature at the four stations, but no significant association between the mean temperature of successive months at the same station. Below-average monthly temperatures tend to be associated with above-average precipitation, particularly in July and August.

During 1916–1933, the intra-monthly variation of both daily maximum and minimum is greatest in April and least in July and August. Within any of the five months, the daily maxima are more variable than the minima. There is a significant correlation between the daily maxima and minima within months (which however diminishes progressively from April to August), and between the mean maximum and mean minimum of April, May and August in different years. The frequency distributions of the 18 years' daily maxima and minima have individual characteristics for each of the five months, which show a generally similar seasonal trend at the four stations. Seasonal trend in the daily range is much less than that in the mean temperature.

The hourly temperature at Swift Current, averaged over four years, attains its maximum at 3 p.m. in all five months studied. The hour of average minimum varies from 6 a.m. in April to 4 a.m. in June. In each month the hours with below-average are in excess of those with above-average temperatures, but this inequality is more pronounced in spring than in summer. The mean of the daily maximum and minimum may sometimes deviate considerably from the mean of the 24 hourly observations.

In an earlier communication (4), the writer discussed certain features of the precipitation statistics for selected meteorological stations in central and southern Saskatchewan and Alberta. Observations of air temperature during the months of the growing season, recorded at these stations and published by the Meteorological Service of Canada (7) are now examined in a similar manner.

The temperature data in question were recorded by thermometers placed in the usual standard screens at a specified height above ground level. It is true that from the agricultural point of view, such data are in some respects inadequate, and may be usefully supplemented by the readings of instruments freely exposed at various levels (3, 9, 10). They do, however, provide a comparable series of standard observations, characteristic of each station.

[1] *Manuscript received August 9, 1937.*

Contribution from the Division of Biology and Agriculture, National Research Laboratories, Ottawa. Published as Paper No. 122 of the Associate Committee on Grain Research of the National Research Council of Canada and the Dominion Department of Agriculture.

[2] *Statistician, National Research Laboratories, Ottawa.*

Annual Variation in Seasonal and Monthly Averages

A study was made of the annual variations in air temperature at four stations, namely, Edmonton (lat. 53° 33′ N., long. 113° 30′ W., alt. 2158 ft.) and Calgary (51°2′ N., 114° 2′ W., 3428 ft.) in central and southern Alberta respectively, and Battleford (52° 41′ N., 108° 20′ W., 1592 ft.) and Swift Current (50° 20′ N., 107° 45′ W., 2392 ft.) in central and southern Saskatchewan.

Secular Trend

An examination of long-time records from various parts of the world made by Kincer (6) led him to the interesting conclusion that the trend of mean annual temperature in the middle latitudes of the northern hemisphere has been definitely upward for more than half a century. The American data (from eastern and mid-western stations) further indicated that the upward trend in the annual means was largely due to a progressive moderation of autumn and winter temperatures, and to a smaller extent to a rise in those for the spring period. During the summer, on the other hand, variations

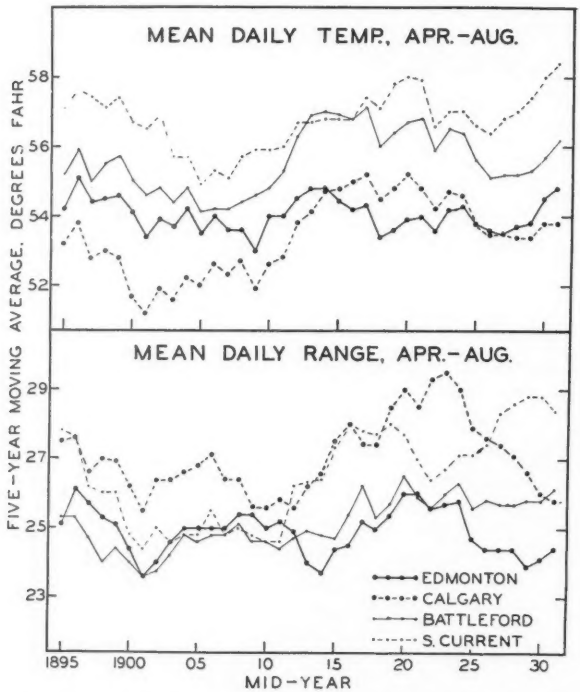


FIG. 1. *Five-year moving average of mean temperature (upper portion) and mean daily range (lower portion) April 1 to August 31, at Edmonton (central Alberta), Calgary (southern Alberta), Battleford (central Saskatchewan) and Swift Current (southern Saskatchewan), 1893–1933.*

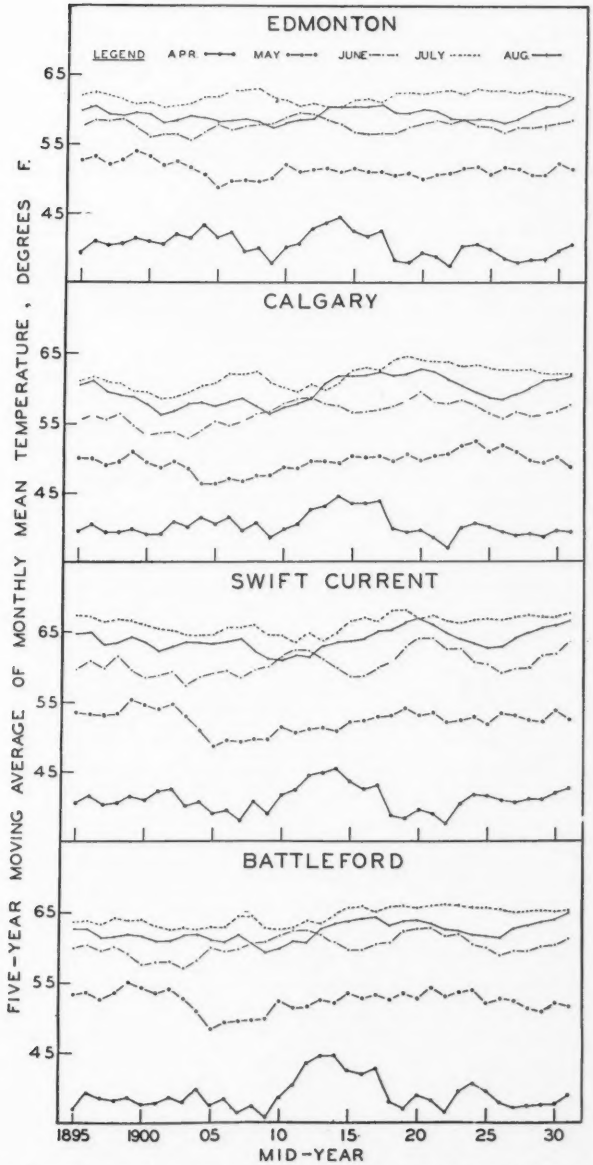


FIG. 2. *Five-year moving averages of monthly mean temperature at Edmonton (central Alberta), Calgary (southern Alberta), Battleford (central Saskatchewan) and Swift Current (southern Saskatchewan), 1893–1933.*

in the 20-year moving average employed by Kincer were for the most part confined to alternating intervals, of irregular length, above and below the average for the entire period covered by the records, this season contributing least to the long-time trend.

Fig. 1 (upper portion) shows the course of a five-year moving average of mean temperature (average of daily maxima and minima) for the spring and summer months, April 1 to August 31, at the above four Canadian stations over the years 1893 to 1933. The moving average has a rather narrow range of variation (about 4° F.) at each station, but within these limits both short- and long-term variation with time is discernible. Over the 41-year period as a whole, the general trend is slightly upward at Calgary, Battleford and Swift Current. At Edmonton, on the other hand, the short-term alternations seem to have taken place about a very stable long-time mean.

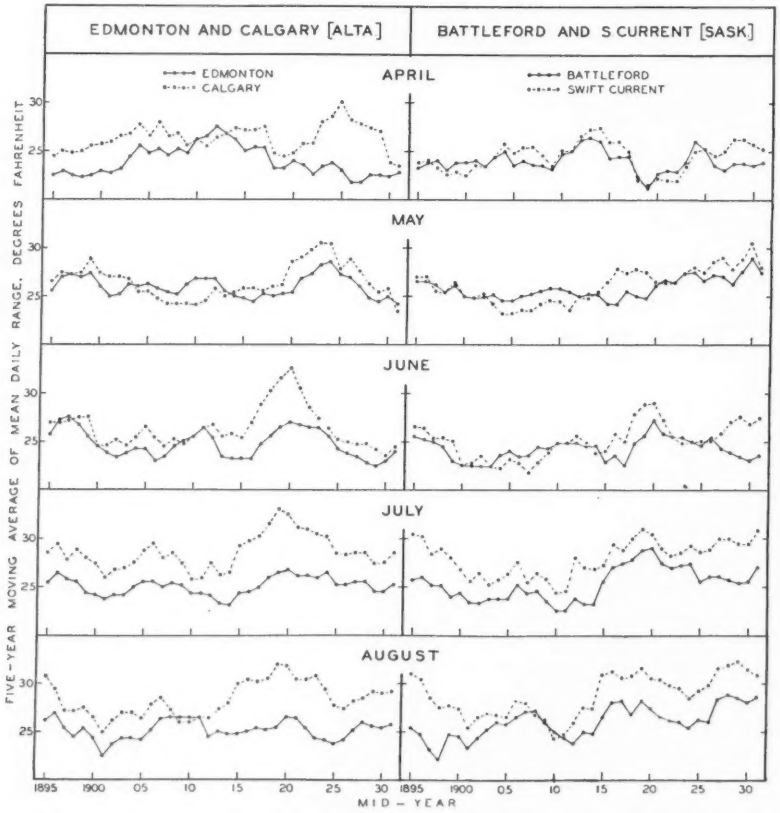


FIG. 3. *Five-year moving averages of monthly mean daily range in temperature at Edmonton (central Alberta), Calgary (southern Alberta), Battleford (central Saskatchewan) and Swift Current (southern Saskatchewan), 1893–1933.*

The short-term variations are irregular in both phase and amplitude, but it is possible nevertheless that they may be connected to some extent with the rather complex fluctuations in the constant of solar radiation, recently described by Abbott (1).

The lower portion of Fig. 1 shows the course of a similar five-year moving average of the mean daily range in temperature for the same five-month period. This quantity proved to have been slightly more variable than the mean temperature itself, the maximum range of fluctuation of the moving average at an individual station being 5° F. Here also there is some indication of short-term variation, three irregular cycles of high and low values being traversed during the 41-year period.

Fig. 2 shows the five-year moving averages of mean temperature for the individual months. At all four stations, the moving averages for April and May show the most pronounced short-term fluctuations. In June, July and August such recurrent oscillations are smaller (moreover, those for each month seem to be largely independent) but the indication of a slight long-time trend is more definite, particularly at Calgary and Swift Current.

A different situation prevails in the case of the monthly mean daily range. At each station the moving average of this quantity shows variations with time in all five months, illustrated in Fig. 3, but the short-term fluctuations are just as pronounced in summer as in spring, if not more so.

Frequency Distribution of Seasonal and Monthly Averages

As only 41 years' observations were available, the characteristics of the frequency distribution of the annual values could not usefully be examined in any detail.

Table I (left portion) shows the distribution, between two-degree class intervals, of the four series of 41 annual values of mean temperature for the five-month period April 1–August 31. At all four stations, the annual five-month averages tend to be concentrated about certain modal values, rather than to occur with approximately equal frequency over the whole range of variation. There is also at all stations a disposition towards asymmetry in the frequency distribution, a majority of the observations falling in the upper part of the range of variation. The general level of April–August mean temperature is slightly higher at the more continental Saskatchewan stations than at the two Alberta ones. The effect of latitude may also be discerned in the observations at Battleford and Swift Current, but in the case of Edmonton and Calgary this factor seems to be more than offset by the difference in altitude. The total range of annual variation is seen to be greatest at Swift Current and least at Edmonton.

A similar classification of the mean daily range in temperature during the period April 1 to August 31 of each of the 41 years is shown in the right half of Table I. This quantity also exhibits modality and a tendency towards asymmetry of distribution, the lower values being on the whole the more

TABLE I

FREQUENCY DISTRIBUTION OF ANNUAL VALUES OF MEAN DAILY TEMPERATURE AND MEAN DAILY RANGE, APRIL 1–AUGUST 31, AT METEOROLOGICAL STATIONS IN CENTRAL AND SOUTHERN ALBERTA AND SASKATCHEWAN, 1893–1933

Mean daily temperature, April 1–August 31					Mean daily range, April 1–August 31				
Class interval, °F.	Edmonton	Calgary	Battleford	Swift Current	Class interval, °F.	Edmonton	Calgary	Battleford	Swift Current
48.0 – 49.9		2			20.0 – 21.9	1			
50.0 – 51.9	4	7	1	1	22.0 – 23.9	11	3	12	6
52.0 – 53.9	12	14	8	2	24.0 – 25.9	21	9	16	10
54.0 – 55.9	21	14	11	9	26.0 – 27.9	6	14	12	15
56.0 – 57.9	4	4	17	16	28.0 – 29.9	2	12	1	6
58.0 – 59.9			4	11	30.0 – 31.9		3		4
60.0 – 61.9				2					
41-year average, °F.	54.1	53.4	55.6	56.8	41-year average, °F.	24.8	27.0	25.2	26.6

numerous. The 41-year average of the five-month mean daily range is higher at the two southern stations, Calgary and Swift Current, than at Edmonton and Battleford.

Fig. 4 shows the frequency distribution of the individual monthly means, the class interval being 4° F. for April and 2° F. for May, June, July and August. All the frequency distributions show some degree of modality, and the seasonal diminution in annual variability at each station from April to July is quite marked. This is the reverse of the situation with respect to monthly precipitation, which was least variable in April and fluctuated most from year to year in June and July (4). In all five months the annual variation is less at Edmonton (central Alberta) than at any of the other stations. Table II summarizes the average values and range of variation of the monthly means.

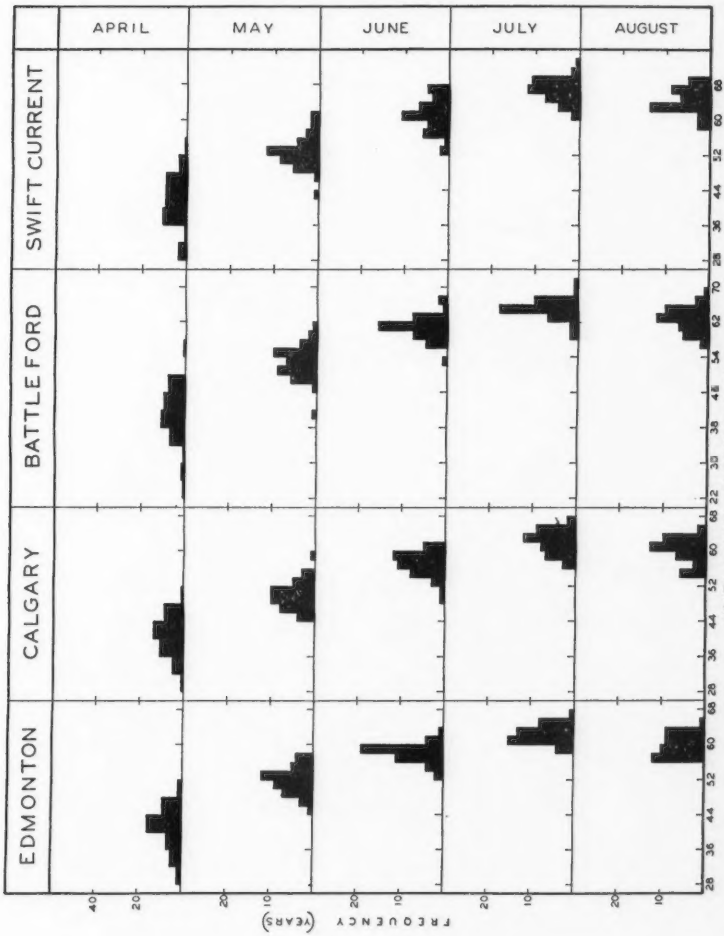


FIG. 4. *Frequency distribution of monthly mean temperature at Edmonton (central Alberta), Calgary (southern Alberta), Battleford (central Saskatchewan) and Swift Current (southern Saskatchewan), 1893–1933.*

TABLE II

MEAN DAILY TEMPERATURE (°F.) BY MONTHS AT METEOROLOGICAL STATIONS IN CENTRAL AND SOUTHERN ALBERTA AND SASKATCHEWAN, 1893–1933

Station	April			May			June			July			August		
	Average 1893–1933	Max.	Min.	Average 1893–1933	Max.	Min.	Average 1893–1933	Max.	Min.	Average 1893–1933	Max.	Min.	Average 1893–1933	Max.	Min.
Edmonton	40.3	49	28	51.3	57	44	57.5	62	52	61.8	66	58	59.4	65	56
Calgary	40.0	49	29	49.3	58	44	56.3	61	50	61.5	66	56	59.6	65	54
Battleford	38.8	52	23	52.3	60	43	60.1	66	52	64.4	70	58	62.3	69	57
Swift Current	41.0	52	31	52.3	60	43	60.5	66	53	66.2	72	60	64.0	68	58

TABLE III

MEAN DAILY RANGE IN TEMPERATURE (°F.) BY MONTHS AT METEOROLOGICAL STATIONS IN CENTRAL AND SOUTHERN ALBERTA AND SASKATCHEWAN, 1893–1933

Station	April			May			June			July			August		
	Average 1893–1933	Max.	Min.	Average 1893–1933	Max.	Min.	Average 1893–1933	Max.	Min.	Average 1893–1933	Max.	Min.	Average 1893–1933	Max.	Min.
Edmonton	23.8	32	17	25.8	32	21	24.7	31	21	25.1	29	21	25.2	32	19
Calgary	26.0	33	17	26.3	33	20	26.3	36	18	28.6	36	21	28.6	35	20
Battleford	23.8	30	17	25.9	31	21	24.4	31	18	25.6	32	19	26.3	32	14
Swift Current	24.3	32	16	26.2	36	19	25.3	33	16	28.3	36	19	29.0	36	19

A similar treatment of the monthly values of mean daily range is shown in Fig. 5 and Table III, the class interval in Fig. 5 being, however, 2° F. for all months. Here again values in the neighborhood of the average tend to be the more numerous, and the annual variation of the monthly means is

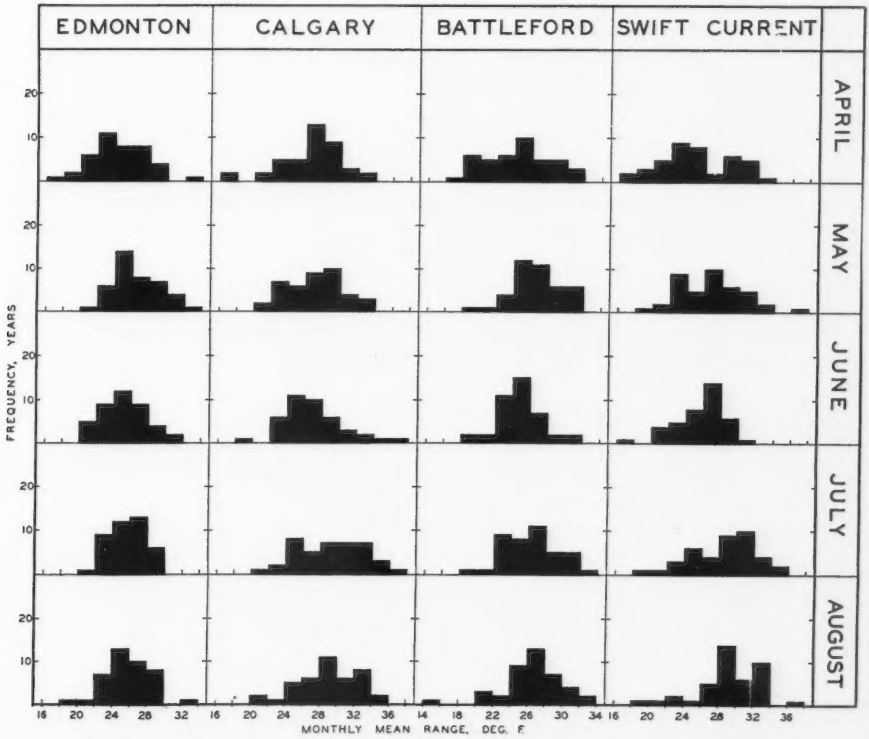


FIG. 5. *Frequency distribution of monthly mean daily range in temperature at Edmonton (central Alberta), Calgary (southern Alberta), Battleford (central Saskatchewan) and Swift Current (southern Saskatchewan), 1893–1933.*

on the whole least at Edmonton and Battleford and greatest at Calgary and Swift Current. The 41-year averages of mean daily range (Table III) are in general slightly higher for the summer than for the spring months. There is however no diminution of the annual variability of the values for the summer as compared to those for the spring months; in fact the former show, if anything, greater variation from year to year.

INTRA- AND INTER-MONTHLY CORRELATIONS

In the writer's previous study of the precipitation statistics for this area (4), it was found that there was a significant association in the total of spring and summer precipitation in the four districts, central and southern Saskat-

chewan and Alberta, but that the degree of correlation was only moderate ($r = 0.3$ to 0.5), leading to the conclusion that the simultaneous occurrence of extremely dry or wet seasons over the whole area may be expected to be infrequent. As anticipated, there is a considerably closer association between the annual variations in monthly mean temperature, all the inter-station coefficients in Table IV exceeding the 1% point. On the whole, inter-station

TABLE IV

INTER-STATION CORRELATION COEFFICIENTS (r) OF ANNUAL MONTHLY MEAN TEMPERATURE, 1893–1933

Stations		April	May	June	July	August
Edmonton	× Calgary	0.92	0.78	0.82	0.80	0.81
	× Battleford	.77	.86	.85	.55	.82
	× Swift Current	.86	.81	.75	.63	.71
Calgary	× Swift Current	.86	.75	.63	.74	.82
	× Battleford	.88	.75	.87	.74	.82
Battleford	× Swift Current	.91	.88	.81	.69	.84

Value of r at 5% point = 0.31.
Value of r at 1% point = 0.40.

correlation is greatest in April, the month of most pronounced variations in temperature from year to year of the five considered, and least in July, the month of highest mean temperature but lowest annual variability. In general the north-south correlations (Edmonton × Calgary and Battleford × Swift Current) are higher than the east-west ones.

The foregoing correlation does not however extend to the mean temperature of successive months at the same station, all the inter-monthly coefficients listed in Table V being small, only three out of 40 exceeding the

TABLE V

INTER-MONTHLY CORRELATION COEFFICIENTS (r) OF MONTHLY MEAN TEMPERATURE, 1893–1933

Months		Edmonton	Calgary	Battleford	Swift Current
April	× May	0.20	0.28	0.17	0.23
	× June	.13	.17	.11	.25
	× July	−.12	.00	−.18	−.04
	× August	.22	.12	.13	−.04
May	× June	−.11	.02	−.04	.04
	× July	−.10	.07	.05	.35
	× August	.19	.19	.26	.25
June	× July	−.14	.22	.15	.17
	× August	−.02	.25	.07	.14
July	× August	−.02	.39	.36	.22

Value of r at 5% point = 0.31.
Value of r at 1% point = 0.40.

5% point and none attaining the 1% point. It would seem therefore that over the 41-year period as a whole, the mean temperature of the five individual months fluctuated independently from year to year. This does not necessarily imply that an above-average mean temperature for June, for example, was never followed by an above-average mean for July, but does indicate that such situations did not occur more frequently than would be expected from chance combinations.

Association between the fluctuations from year to year of the precipitation and mean temperature of the same month was investigated by the calculation of the correlation coefficients shown in Table VI. As the study of rainfall (4) had already indicated that there was a correlation between total precipitation and the number of rainy days per month, and as on rainy days there is at least a temporary interruption of solar radiation, some degree of connection between precipitation and monthly mean temperature might be anticipated.

TABLE VI

COEFFICIENTS OF INTER-ANNUAL CORRELATION BETWEEN PRECIPITATION (INCHES OF RAIN) AND MEAN TEMPERATURE (°F.), BY MONTHS, AT METEOROLOGICAL STATIONS IN CENTRAL AND SOUTHERN ALBERTA AND SASKATCHEWAN, 1893-1933

Station	April	May	June	July	August
Edmonton	0.02	0.03	−0.05	−0.42**	−0.31
Calgary	− .20	− .41*	− .49**	− .40*	− .52**
Battleford	− .12	.06	− .15	− .38*	− .40*
Swift Current	− .10	− .32*	− .15	− .37*	− .37*

Exceeds 5% point (0.31).
**Exceeds 1% point (0.40).*

The results in Table VI are as a whole consistent with this supposition. Seventeen of the 20 coefficients listed are negative, indicating that increased precipitation tended to be associated with a lower monthly mean temperature, and the three positive values are all insignificant, the largest being only 0.06. The degree of correlation indicated is however at best only moderate, and is further characterized by a marked seasonal incidence. Considered individually, the coefficients for April at all four stations are insignificant. Two of those for May, and one for June, exceed the 5% point. On the other hand, all of those for July and August may be regarded as significant, and four of the eight attain or exceed the 1% point.

Characteristics of Daily Observations

At the time that this study was begun, records of the daily observations at the four foregoing stations for the years 1916 to 1933 inclusive were available in published form (7). These were examined as described below.

Intra- and Inter-annual Variation of Daily Observations by Months

The analysis of variance procedure (2) was applied to the observations recorded for each station. In this way the total daily variance of the mean, maximum, minimum and range in temperature of each month during the 18 years was subdivided as shown in Tables VII to X into one portion arising from differences in the averages of the same month (*e.g.*, April) in different years, and another portion due to daily deviations from the average of the individual months within years. Each of the four tables in question is thus deduced from a total of 11,016 daily observations.

In each table the observations for all five months at all four stations have yielded greater mean squares between years than within years, and with but one exception these differences in variance are individually significant. It would seem, therefore, that the average maximum, minimum, mean and range of the same month in different years are determined in part by the operation of factors additional to those causing variation from day to day within months. The mean squares within years provide a direct measure of the variation of the four temperature characteristics from day to day, based on 18 years' experience at each station. To facilitate comparisons, the corresponding standard deviations are brought together in Table XI.

Although the standard deviations of daily maxima and minima are in general slightly higher for the southern than for the central stations, and for the Saskatchewan than the Alberta ones, there are no pronounced differences between stations in respect of the intra-monthly variation of any of the four series of daily observations. Within stations, on the other hand, the daily maximum temperatures recorded for all five months are seen to have been more variable than the corresponding daily minima. The intra-monthly daily variation of both these quantities, as also that of the mean and range, shows an appreciable seasonal variation. The variability of maximum, minimum and mean is highest in April and lowest in July and August. In the case of the daily range, however, the lowest variability is attained in June and July. Furthermore, the differences between months in the standard deviation of daily range are definitely smaller than the corresponding differences in the standard deviation of daily maximum, minimum or mean. This is indicative of a closer correlation between the maximum and minimum temperature of the same day in the earlier part of the season.

Intra- and Inter-annual Correlation Between Daily Maxima and Minima

The values of the correlation coefficient r, specifying the degree of association between daily maximum and minimum temperature by months both within and between years, were readily deduced from the mean squares given in Tables VIII, IX and X. Denoting the daily maximum temperature by t_1, the daily minimum by t_2, the daily range by t_1-t_2, and any mean square

TABLE VII

ANALYSIS OF VARIANCE OF MEAN DAILY TEMPERATURE (°F.), BY MONTHS, 1916–1933

Station	Variance	April		May		June		July		August	
		D.F.	Mean sq.	D.F.	Mean sq.	D.F.	Mean sq.	D.F.	Mean sq.	D.F.	Mean sq.
Edmonton	Between years	17	586.4**	17	173.4**	17	70.1*	17	57.8*	17	141.4**
	Within years	522	87.0	540	52.6	522	39.7	540	30.7	540	29.7
Calgary	Between years	17	581.1**	17	211.0**	17	110.4**	17	64.2**	17	119.0**
	Within years	522	77.7	540	53.3	522	40.2	540	30.2	540	32.6
Battleford	Between years	17	680.9**	17	257.5**	17	164.9**	17	112.7**	17	117.8**
	Within years	522	94.6	540	63.1	522	42.6	540	30.4	540	34.5
Swift Current	Between years	17	523.7**	17	322.9**	17	330.8**	17	84.5**	17	188.1**
	Within years	522	91.6	540	69.7	522	51.0	540	40.2	540	39.0

**Exceeds mean square within years, 5% level of significance.*
***Exceeds mean square within years, 1% level of significance.*

TABLE VIII

ANALYSIS OF VARIANCE OF MAXIMUM DAILY TEMPERATURE (°F.), BY MONTHS, 1916–1933

Station	Variance	April		May		June		July		August	
		D.F.	Mean sq.	D.F.	Mean sq.	D.F.	Mean sq.	D.F.	Mean sq.	D.F.	Mean sq.
Edmonton	Between years	17	1055.8**	17	353.1**	17	140.6**	17	166.9**	17	257.2**
	Within years	522	130.7	540	92.9	522	66.2	540	55.8	540	60.2
Calgary	Between years	17	970.8**	17	619.1**	17	357.9**	17	308.4**	17	280.5**
	Within years	522	144.6	540	97.8	522	80.0	540	59.8	540	73.1
Battleford	Between years	17	1318.9**	17	450.3**	17	269.2**	17	125.9**	17	217.4**
	Within years	522	137.2	540	102.2	522	73.1	540	54.3	540	66.0
Swift Current	Between years	17	915.3**	17	684.2**	17	555.6**	17	253.2**	17	323.6**
	Within years	522	149.6	540	110.2	522	86.0	540	67.4	540	72.2

**Exceeds mean square within years, 5% level of significance.*
***Exceeds mean square within years, 1% level of significance.*

TABLE IX

ANALYSIS OF VARIANCE OF MINIMUM DAILY TEMPERATURE, (°F.), BY MONTHS, 1916–1933

Station	Variance	April		May		June		July		August	
		D.F.	Mean sq.	D.F.	Mean sq.	D.F.	Mean sq.	D.F.	Mean sq.	D.F.	Mean sq.
Edmonton	Between years	17	349.7**	17	97.6**	17	93.7**	17	47.6*	17	103.8**
	Within years	522	73.7	540	45.9	522	40.8	540	29.4	540	31.4
Calgary	Between years	17	430.2**	17	79.1**	17	99.5**	17	45.4	17	100.8**
	Within years	522	62.5	540	38.8	522	29.5	540	28.5	540	28.2
Battleford	Between years	17	388.4**	17	236.1**	17	194.7**	17	105.8**	17	105.7**
	Within years	522	89.2	540	60.3	522	42.6	540	31.8	540	37.2
Swift Current	Between years	17	338.8**	17	258.7**	17	245.4**	17	72.1*	17	148.0**
	Within years	522	72.7	540	65.1	522	47.1	540	41.9	540	39.7

*Exceeds mean square within years, 5% level of significance.
**Exceeds mean square within years, 1% level of significance.

TABLE X

ANALYSIS OF VARIANCE OF DAILY RANGE IN TEMPERATURE (°F.), BY MONTHS, 1916–1933

Station	Variance	April		May		June		July		August	
		D.F.	Mean sq.	D.F.	Mean sq.	D.F.	Mean sq.	D.F.	Mean sq.	D.F.	Mean sq
Edmonton	Between years	17	297.5**	17	212.7**	17	168.9**	17	191.0**	17	158.1**
	Within years	522	67.5	540	68.9	522	56.2	540	48.9	540	63.7
Calgary	Between years	17	585.9**	17	493.0**	17	463.5**	17	450.1**	17	290.7**
	Within years	522	91.6	540	78.0	522	61.0	540	56.7	540	73.2
Battleford	Between years	17	485.9**	17	275.8**	17	273.5**	17	304.5**	17	186.1**
	Within years	522	72.0	540	70.2	522	62.2	540	52.0	540	70.1
Swift Current	Between years	17	417.6**	17	563.5**	17	259.3**	17	326.1**	17	189.8**
	Within years	522	81.0	540	74.3	522	61.4	540	58.2	540	68.9

**Exceeds mean square within years, 5% level of significance.*
***Exceeds mean square within years, 1% level of significance.*

TABLE XI

INTRA-MONTHLY STANDARD DEVIATION (°F.) OF DAILY MEAN, MAXIMUM, MINIMUM, AND RANGE IN TEMPERATURE, 1916–1933

Month	Edmonton				Calgary				Battleford				Swift Current			
	Mean	Max.	Min.	Range	Mean	Max.	Min.	Range	Mean	Max.	Min.	Range	Mean	Max.	Min.	Range
April	9.3	11.4	8.6	8.2	8.8	12.0	7.9	9.6	9.7	11.7	9.4	8.5	9.6	12.2	8.5	9.0
May	7.3	9.6	6.8	8.2	7.3	9.9	6.2	8.8	8.0	10.1	7.8	8.4	8.4	10.5	8.1	8.6
June	6.2	8.1	6.4	7.5	6.3	8.9	5.4	7.8	6.5	8.6	6.5	7.9	7.1	9.3	6.9	7.8
July	5.5	7.5	5.4	7.0	5.5	7.7	5.3	7.5	5.5	7.4	5.6	7.2	6.3	8.2	6.5	7.6
August	5.4	7.8	5.6	8.0	5.7	8.6	5.3	8.6	5.9	8.1	6.1	8.4	6.2	8.5	6.3	8.3

by s^2, it is well known that

$$s^2_{t_1-t_2} = s^2_{t_1} + s^2_{t_2} - 2r_{t_1t_2} \cdot s_{t_1}s_{t_2}$$

whence

$$r_{t_1t_2} = \frac{s^2_{t_1} + s^2_{t_2} - s^2_{t_1-t_2}}{2s_{t_1}s_{t_2}}.$$

Substituting the appropriate mean squares in the foregoing expression, the values of r shown in Tables XII and XIII were obtained.

Table XII shows for each of the five months the intra-monthly correlation coefficients computed from the mean squares within years. All of these are statistically significant, the 1% point for the shorter months (30 days per

TABLE XII

INTRA-MONTHLY CORRELATION COEFFICIENTS (r) BETWEEN DAILY MAXIMUM AND MINIMUM TEMPERATURE (°F.)

Station	April	May	June	July	August
Edmonton	0.70	0.50	0.49	0.45	0.32
Calgary	.61	.48	.50	.38	.31
Battleford	.70	.59	.48	.41	.33
Swift Current	.68	.60	.56	.49	.40

Value of r at 1% point $\leqslant 0.11$

annum, 521 degrees of freedom) being $r = 0.11$. There is therefore a definite tendency within each month during the period considered for above-average daily maximum temperatures to be associated with above-average minima, and below-average maxima with below-average minima. This tendency is however more pronounced in spring than in summer. At all four stations the correlation coefficients decline progressively from April to August, the degree of association indicated in the latter month being very moderate.

The coefficients obtained from the mean squares between years are shown in Table XIII. These indicate the degree of association between the mean daily maximum and mean daily minimum temperature of the specified months from year to year over the period 1916–1933. As the mean squares in this instance are each derived from only 17 degrees of freedom, the resulting

TABLE XIII

INTER-ANNUAL CORRELATION COEFFICIENTS (r) BETWEEN MONTHLY MEAN MAXIMUM AND MINIMUM TEMPERATURES (°F.), 1916–1933

Station	April	May	June	July	August
Edmonton	0.91**	0.64**	0.28	0.13	0.62**
Calgary	.63**	.46	− .02	− .41	.27
Battleford	.85**	.63**	.42	− .32	.45
Swift Current	.75**	.45	.73**	.00	.64**

Value of r at 5% point = 0.47. **Exceeds 5% point.*
Value of r at 1% point = 0.59. ***Exceeds 1% point.*

coefficients are determined with a much lower precision than those of the preceding Table XI, if considered as estimates of the true values characteristic of the climate of the stations rather than as merely descriptive statistics of the particular 18 seasons examined. Even so, there is evidence of a rather pronounced seasonal variation in the inter-annual correlation. The association would seem to be close in April, when the variation in the temperature conditions from year to year may be considerable (Table II); to decline to a minimum in June and July, in which months inter-annual variation is smaller; and to increase again in August. Thus warmer-than-average Aprils tend to be characterized by mean maxima and minima which are both above-average. In mid-summer, on the contrary, this tendency no longer prevails.

In this connection, however, it should be pointed out that during the spring and summer months the minimum temperature recorded for any particular day usually occurs during the early morning hours, with the result that the foregoing correlations are, in effect, between minimum and succeeding maximum rather than between maximum and succeeding minimum. Additional calculations were therefore made in order to determine the latter for two of the four stations, namely Edmonton and Swift Current. The results are given in Tables XIV, XV and XVI.

TABLE XIV

INTER-ANNUAL COEFFICIENTS OF CORRELATION (r) BETWEEN MONTHLY MEAN MAXIMUM AND SUCCEEDING MINIMUM TEMPERATURES (°F.), 1916–1933

Station	April	May	June	July	August
Edmonton	0.91**	0.61**	0.28	0.17	0.65**
Swift Current	.62**	.44	.74**	− .02	.65**

Value of r at 5% point = 0.47. **Exceeds 5% point.*
Value of r at 1% point = 0.59. ***Exceeds 1% point.*

TABLE XV

INTRA-MONTHLY COEFFICIENTS OF CORRELATION (r) BETWEEN DAILY MAXIMUM AND SUCCEEDING MINIMUM TEMPERATURES (°F.), 1916–1933

Station	April	May	June	July	August
Edmonton	0.74	0.68	0.60	0.60	0.54
Swift Current	.72	.66	.64	.58	.58

Value of r at 1% point $\leqslant 0.11$.

TABLE XVI

COEFFICIENTS OF REGRESSION (b) OF SUCCEEDING MINIMUM ON DAILY MAXIMUM TEMPERATURE, (°F.), 1916–1933

Station	April	May	June	July	August
Edmonton	0.55±0.02	0.48±0.02	0.46±0.03	0.44±0.02	0.40±0.03
Swift Current	.50± .02	.51± .02	.47± .02	.47± .03	.43± .03

As might be expected, the correlation between mean monthly maximum and minimum determined from the 17 degrees of freedom between years is not significantly affected, and the remarks made with reference to the preceding Table XIII apply also to the inter-annual coefficients in Table XIV.

The intra-monthly correlations, based on 521 residual degrees of freedom for April and June, and 539 for May, July and August, are given in Table XV. All again exceed the 1% point, and, as expected, the coefficients in this table are uniformly higher than the corresponding ones in Table XI. As before, however, the degree of association indicated is highest for the spring months, and only moderate for the summer.

Table XVI contains the intra-monthly regression coefficients of minimum temperature on preceding daily maximum for both Edmonton and Swift Current. These range from 0.40 to 0.55° F., indicating that the amplitude of associated variations in the minima was on the average about half that of the fluctuations in daily maxima. Within any month, the regression coefficients for the two stations do not differ significantly, but at both places they are somewhat higher for spring than for summer. Thus at Edmonton, a 10-degree difference in daily maxima during April resulted on the average in a difference of 5.5° in the subsequent minima, whereas in August the corresponding average difference in the minima was only 4.0°.

Frequency Distribution of Daily Observations

The frequency distribution between 4° F. class intervals of the daily maximum and minimum readings for each month at the four stations during the 18-year period is represented by means of histograms in Fig. 6. Table XVII lists the numerical values of certain statistics descriptive of the individual distributions, computed in each case from the ungrouped data.

Five statistics are given in each case. The first of these is simply the arithmetic mean of the aggregate of observations, 540 or 558 in number, depending on whether the month in question comprises 30 or 31 days. Next follow the second (m_2), third (m_3) and fourth (m_4) moments about the mean, *i.e.*, the mean square, mean cube and mean fourth power of the 540 or 558 deviations from the arithmetic mean. The mean square deviation or variance (m_2) is indicative of the extent of dispersion in the distribution, whilst the pure numbers $\sqrt{B_1} = \frac{m_3}{m_2^{3/2}}$ and $B_2 = \frac{m_4}{m_2^2}$, also given in Table XVII, permit comparisons to be made between the symmetry and modality (*i.e.*, the tendency of the observations to cluster numerously about some modal value) of distributions of different absolute dispersion. If the observations follow exactly the "Normal" law of frequency $\sqrt{B} = 0$ and $B_2 = 3$. Tables have been published by E. S. Pearson (8) enabling the significance of observed deviations from these values, in samples of different sizes, to be tested.

In addition to the average seasonal trend of the maximum and minimum, there may also be observed from the two columns of means in Table XVII a

further effect attributable to the interacting differences in latitude and elevation between Edmonton and Calgary. The mean minimum temperature for each of the five months is lower for Calgary than for Edmonton, whereas the mean maximum is higher, except for May. On the other hand, there is little difference between the mean minima for Battleford and Swift Current, excepting those for April, when the value for the southern station is the higher. The five mean maxima are again consistently higher for Swift Current than for Battleford.

The coefficients $\sqrt{B_1}$ and B_2 exhibit certain trends over the five-month period. In the case of the daily minima, $\sqrt{B_1}$ is significantly negative at all four stations for April. The asymmetry of the four distributions is evident

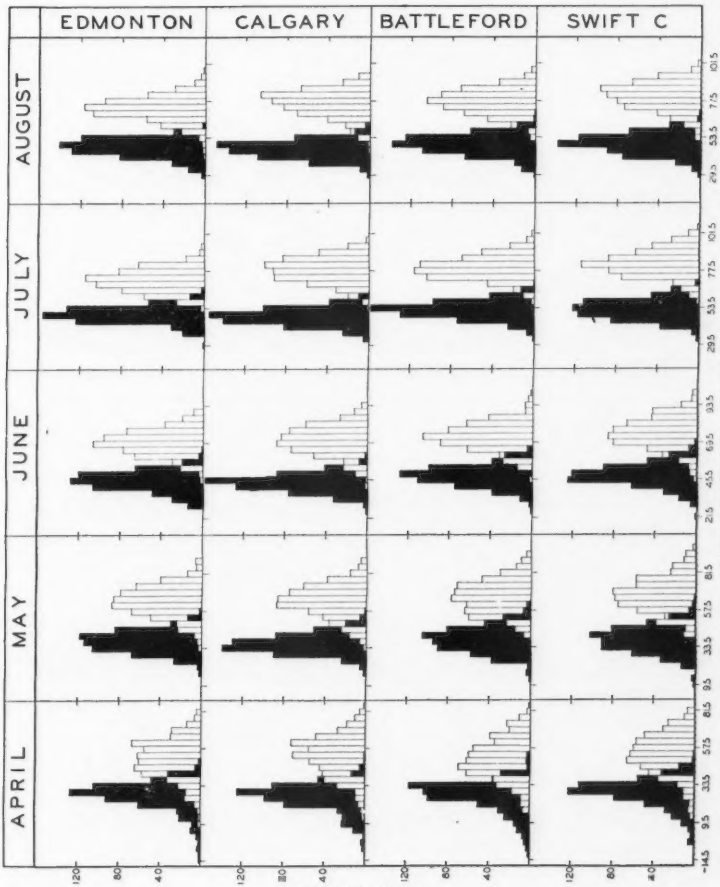


FIG. 6. *Frequency distribution of daily maximum (open columns) and minimum (solid columns) temperatures at Edmonton (central Alberta), Calgary (southern Alberta), Battleford (central Saskatchewan) and Swift Current (southern Saskatchewan), 1916–1933.*

TABLE XVII

STATISTICS OF FREQUENCY DISTRIBUTION OF DAILY MAXIMUM AND MINIMUM AIR TEMPERATURES (°F.) AT METEOROLOGICAL STATIONS IN CENTRAL AND SOUTHERN ALBERTA AND SASKATCHEWAN, 1916–1933

Month		Daily minima						Daily maxima					
		Mean	Second moment (m_2)	Third moment (m_3)	Fourth moment (m_4)	$\sqrt{B_1}$	B_2	Mean	Second moment (m_2)	Third moment (m_3)	Fourth moment (m_4)	$\sqrt{B_1}$	B_2
April—	Edmonton	27.9	82.25	−819.70	36,934.63	−1.099**	5.460**	50.8	159.59	−493.83	75,301.11	−0.245*	2.957
	Calgary	26.5	73.99	−461.02	22,229.79	−0.724**	4.061**	52.4	170.30	−590.33	71,421.32	−0.266**	2.463**
	Battleford	26.9	98.43	−865.79	38,235.01	−0.887**	3.946**	50.2	174.14	6.88	82,000.57	0.003	2.704
	Swift Current	28.7	80.91	−528.40	27,703.58	−0.726**	4.232**	52.6	173.44	−650.84	88,272.71	−0.171	2.934
May—	Edmonton	38.0	47.41	54.40	5,993.49	0.167	2.667	63.7	100.62	− 20.66	30,289.25	−0.020	2.992
	Calgary	36.3	40.00	65.31	5,116.61	0.258**	3.198	63.3	113.51	−297.89	43,763.60	−0.239**	3.397
	Battleford	38.9	65.58	29.15	12,027.78	0.055	2.797	65.8	114.14	111.60	32,070.85	0.092	2.462**
	Swift Current	38.5	70.87	− 17.40	15,158.65	−0.029	3.018	66.6	127.53	115.68	44,984.99	0.080	2.766
June—	Edmonton	45.2	42.35	− 45.13	5,180.43	−0.164	2.888	70.0	68.38	− 46.54	12,874.62	−0.092	2.753
	Calgary	43.9	31.66	0.89	2,829.88	0.005	2.823	70.8	89.57	−197.36	23,388.81	−0.233*	2.915
	Battleford	48.1	47.30	− 31.80	6,534.57	−0.098	2.921	72.8	79.17	− 39.83	19,823.98	−0.057	3.163
	Swift Current	48.2	53.25	− 36.45	8,959.74	−0.094	3.160	75.0	100.66	− 74.54	29,970.64	−0.074	2.958
July—	Edmonton	49.5	29.88	− 13.20	2,561.07	−0.081	2.869	75.0	59.13	− 56.75	9,989.20	−0.125	2.857
	Calgary	48.0	28.92	− 9.48	2,245.59	−0.061	2.685*	77.8	67.31	− 34.30	12,116.45	−0.062	2.674*
	Battleford	52.1	34.00	− 21.11	3,401.38	−0.107	2.951	79.2	56.40	32.51	9,647.67	0.078	3.033
	Swift Current	52.4	42.72	2.52	4,816.91	0.009	2.639*	81.9	72.91	10.81	12,913.68	0.017	2.813
August—	Edmonton	47.5	33.55	− 77.16	3,184.45	−0.397**	2.829	72.4	66.06	−144.70	14,622.47	−0.270**	3.351*
	Calgary	46.1	30.40	− 7.92	2,426.02	−0.047	2.625*	75.5	79.30	−344.55	18,098.73	−0.488**	2.878
	Battleford	49.1	39.20	− 51.40	4,496.04	−0.209*	2.926	76.6	70.47	− 88.11	13,711.58	−0.149	2.761
	Swift Current	49.4	42.94	− 43.21	4,960.57	−0.154	2.690*	79.8	79.73	−239.14	17,944.52	−0.336**	2.823

Deviation of $\sqrt{B_1}$ from zero, or of B_2 from 3.000, exceeds 5% point.

**Deviation of $\sqrt{B_1}$ from zero, or of B_2 from 3.000, exceeds 1% point.*

from Fig. 6, the mode being in excess of the mean, and moderately above- and markedly below-average daily minima being more numerous than moderately below- and markedly above-average ones respectively. The high values of B_2 are indicative of a further feature, namely the pronounced modality of the daily minima for this month. Thus at Edmonton the total range of variation by four-degree class intervals is from $-16.5°$ to $+51.5°$ F. or 68°; but the 12-degree interval 23.5° to 35.5° comprises 323 or 60% of the total of 540 daily values. The same 12-degree interval was found to include at Calgary 311 or 58%, at Battleford 319 or 59%, and at Swift Current 312 or 58% of the daily observations. The April daily maxima also show tendencies in the direction of a negatively skewed frequency distribution at three of the four stations, but the values of $\sqrt{B_1}$ indicate that this symptom is relatively less marked than in the case of the daily minima. Furthermore, there is not so pronounced a concentration of the observations within the modal region, all four values of B_2 being below rather than above the Normal value of 3.000, although the deviation from normality is statistically significant in only one instance.

In the succeeding months of May, June and July the variance of both maximum and minimum diminishes progressively; also, the distribution of the daily observations approaches more closely the Normal form, corresponding deviations above and below the mean tending to occur with equal frequency. The August observations on the other hand show a reversion to the negatively skewed distribution of both daily maxima and minima which is characteristic of those for April. In August however the asymmetry is more pronounced in the maxima than in the minima, and the concentration of frequency in the modal region is in general in defect rather than in excess of the Normal expectation. When examined in this way, therefore, each of the five months is seen to have individual temperature characteristics which, for the 18-year period considered, show a generally similar seasonal progression at the stations in all four districts.

Table XVIII lists two temperature attributes of some agricultural interest, namely the percentage of the daily minima falling below 40° F. and the percentage of the daily maxima attaining or exceeding 80° F., and permits comparisons to be made both between months and between stations.

TABLE XVIII

PERCENTAGE OF DAILY MINIMUM AIR TEMPERATURES BELOW 40° F. AND OF DAILY MAXIMA OF 80° F. OR ABOVE, AT METEOROLOGICAL STATIONS IN CENTRAL AND SOUTHERN ALBERTA AND SASKATCHEWAN BY MONTHS, 1916–1933

Month	Minima below 40° F., %				Maxima 80° F. or above, %			
	Edmonton	Calgary	Battleford	Swift Current	Edmonton	Calgary	Battleford	Swift Current
April	93	96	93	91	1	1	1	1
May	58	70	52	53	4	5	10	12
June	17	21	10	10	12	20	23	33
July	4	5	1	1	29	46	47	62
August	9	13	6	6	18	38	38	55

The frequency distribution of the daily mean temperatures (average of maximum and minimum) was also determined for each month and station, and is shown graphically in Fig. 7. The individual daily maxima and minima being positively correlated, the frequency distributions derived from them show seasonal trends in variance, skewness and kurtosis similar to those illustrated in Fig. 6.

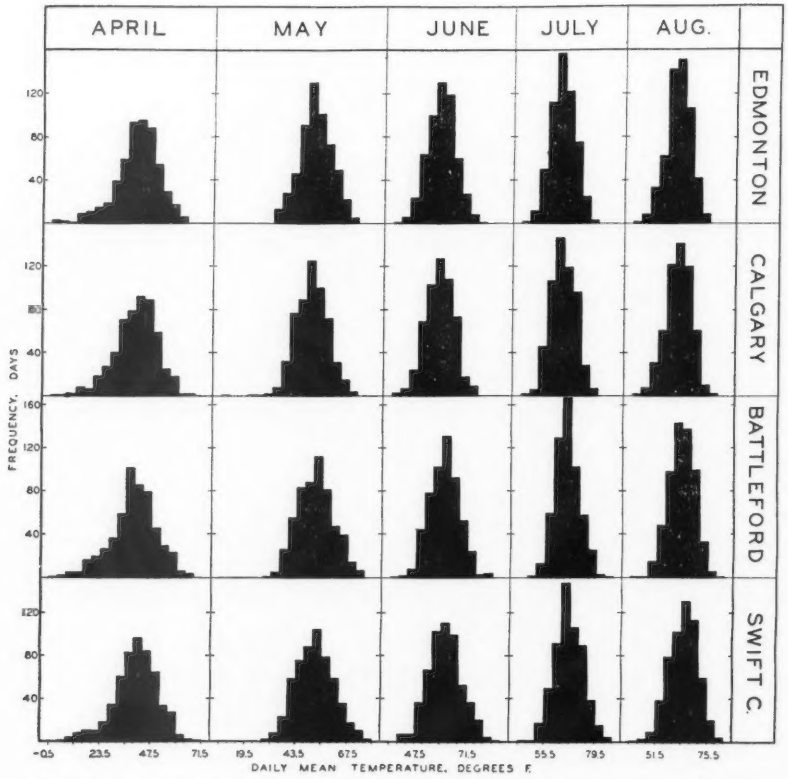


FIG. 7. *Frequency distribution of daily mean temperatures at Edmonton (central Alberta), Calgary (southern Alberta), Battleford (central Saskatchewan) and Swift Current (southern Saskatchewan), 1916–1933.*

In addition to the mean, the daily range in temperature was also calculated from the maxima and minima. The aggregate of observations at all four stations for the 18 years provided a total of 2160 daily values for the months of April and June, and 2232 for each of May, July and August. Table XIX indicates, to the nearest unit, the percentage distribution of these between various class intervals. All five monthly distributions show a concentration of frequency in the central classes, but the modal region tends

TABLE XIX

PERCENTAGE FREQUENCY DISTRIBUTION AND MEAN VALUE OF DAILY RANGE IN AIR TEMPERATURE (°F.) BY MONTHS AT EDMONTON, CALGARY, BATTLEFORD AND SWIFT CURRENT, 1916–1933

Class interval	April	May	June	July	August
0 to 7° incl.	3	2	2	1	1
8 to 11	7	4	3	2	3
12 to 15	11	6	7	5	4
16 to 19	12	10	9	8	8
20 to 23	15	13	17	13	13
24 to 27	15	15	18	17	16
28 to 31	14	16	18	20	17
32 to 35	12	17	14	18	18
36 to 39	7	11	7	10	11
40 to 43	3	4	3	5	6
44 –	2	2	1	2	3
Mean daily range, °F.	24.0	26.9	25.8	28.0	28.0

upward as the season advances, this being accompanied by a decrease in the proportion of smaller daily ranges and an increase in that of the larger ones. It may be noted that the observations for June show a recession from this trend; this is presumably connected with the fact that June is the month of maximum average precipitation in the Plains area. Seasonal change in the average daily range is however much less pronounced than that in the temperature itself. The mean daily temperature at the four stations for 1916–1933 increases from 39.5° F. in April to 64.0° F. in July, but the corresponding variation in the mean daily range is only from 24.0° to 28.0°.

Separate tabulations showed a similar seasonal trend to be characteristic of the observations of daily range at each of the four stations individually, but application of the χ^2 test of homogeneity to the separate tabulations indicated statistically significant differences between stations for each of the five months. These seemed to be attributable mainly to the fact that the mean daily range for each month was higher at Calgary and Swift Current than at Edmonton and Battleford.

Hourly Temperatures at Swift Current

For some years it was the custom of the Meteorological Service of Canada to publish in full the hourly temperatures recorded at a number of stations by automatic instruments. Of the four stations here considered, Swift Current is the only one for which such results were thus available.

DIURNAL VARIATION

The hourly observations at this station during April, May, June, July and August of the years 1922, 1923, 1925 and 1927 were used to compute the average diurnal variation in temperature for each month, shown in Fig. 8 and Table XX. Had the records been complete, each hourly point in the curves would have been the average of 120 daily observations in April and

June, and of 124 in May, July and August. Actually, however, there were some days on which the instrument was temporarily out of order. Whenever this occurred, the observations for the entire day concerned were excluded from the averages.

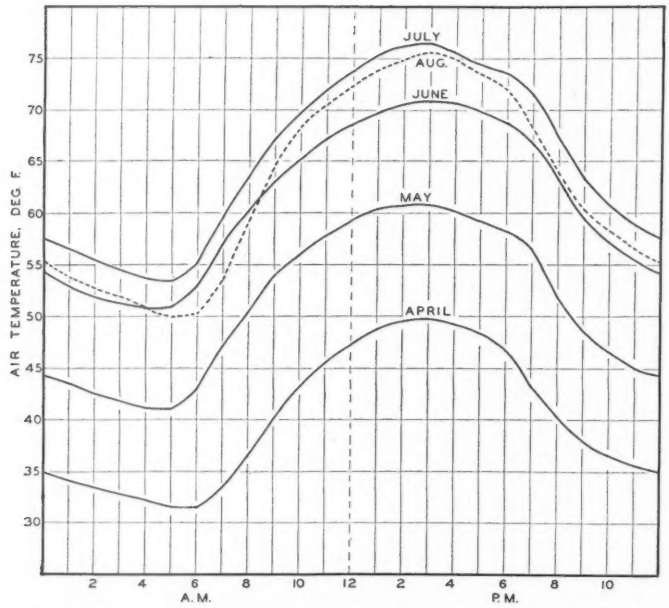


FIG. 8. *Average diurnal temperature curves for five spring and summer months at Swift Current, Saskatchewan. Computed from hourly observations recorded in 1922, 1923, 1925 and 1927.*

In spite of the differences in respect of the general temperature level, the average hourly value attains its maximum at this station at 3 p.m. in all five months. The subsequent decline is seen to be most rapid in the earlier part of the night. By 10 or 11 p.m. a more moderate rate of cooling supervenes, which is maintained until arrested next morning by renewed insolation. The hour of minimum average temperature, being influenced by the time of sunrise, varies from 6 a.m. in April to 4 a.m. in June.

All five diurnal curves are to some extent asymmetrical, the number of hourly intervals with falling temperature being in excess of the number with rising temperature. On the other hand, the average rate of cooling is in consequence slower than the average rate of heating. As is indicated in Table XX, this disproportion is least in evidence in the observations for June, the month of longest day, and most pronounced in those for April.

TABLE XX

HOURLY TEMPERATURE (°F.) AT SWIFT CURRENT, SASKATCHEWAN, BY MONTHS. AVERAGE OF FOUR YEARS' OBSERVATIONS

Hour	April	May	June	July	August
1 a.m.	34.2	43.6	52.8	56.4	53.8
2	33.4	42.6	51.8	55.5	52.7
3	32.8	41.8	51.2	54.5	51.9
4	32.2	41.1	50.7	53.7	50.8
5	31.6	41.0	50.8	53.4	50.0
6	31.5	43.0	53.0	55.2	50.2
7	33.4	47.1	56.7	59.6	53.5
8	36.5	50.5	60.2	63.6	59.2
9	40.1	54.0	63.2	67.2	64.7
10	43.2	56.0	65.2	69.8	68.4
11	45.6	57.8	67.2	72.0	70.5
12	47.3	59.3	68.6	73.7	72.3
1 p.m.	48.8	60.4	69.8	75.4	73.9
2	49.5	60.7	70.6	76.2	74.9
3	49.8	60.8	70.8	76.5	75.6
4	49.3	60.2	70.7	75.6	74.9
5	48.4	59.2	69.8	74.4	73.5
6	46.8	58.2	68.8	73.6	72.0
7	43.4	56.6	66.8	71.5	68.2
8	40.3	51.8	63.2	67.3	63.7
9	38.0	48.6	59.4	63.2	60.2
10	36.6	46.6	57.2	60.7	58.3
11	35.6	45.0	55.4	58.8	56.4
12	34.9	44.2	54.2	57.5	55.2
No. hourly intervals with rising temp.	9	10	11	10	9
No. hourly intervals with falling temp.	15	14	13	14	15
Average hourly rise	2.0°	2.0°	1.8°	2.3°	2.8°
Average hourly fall	1.2°	1.4°	1.5°	1.6°	1.7°

FREQUENCY DISTRIBUTION OF HOURLY TEMPERATURES

Fig. 9 shows diagrammatically the percentage frequency distribution, between 4° F. class intervals, of the aggregate of hourly temperatures recorded during each of the five months of the four years considered. The full complement of observations for each distribution is 720 in the case of April and June, and 744 in the case of May, July and August, but as before, whenever the instrument was temporarily out of order, the records for the entire day concerned were excluded.

The general seasonal trend of temperature, reaching its maximum in July, is of course well in evidence, but it is also clear that in the spring months (April and May) there may be an appreciable annual variation in the aggregate of hourly values. The other months studied show on the whole more consistency over the four years.

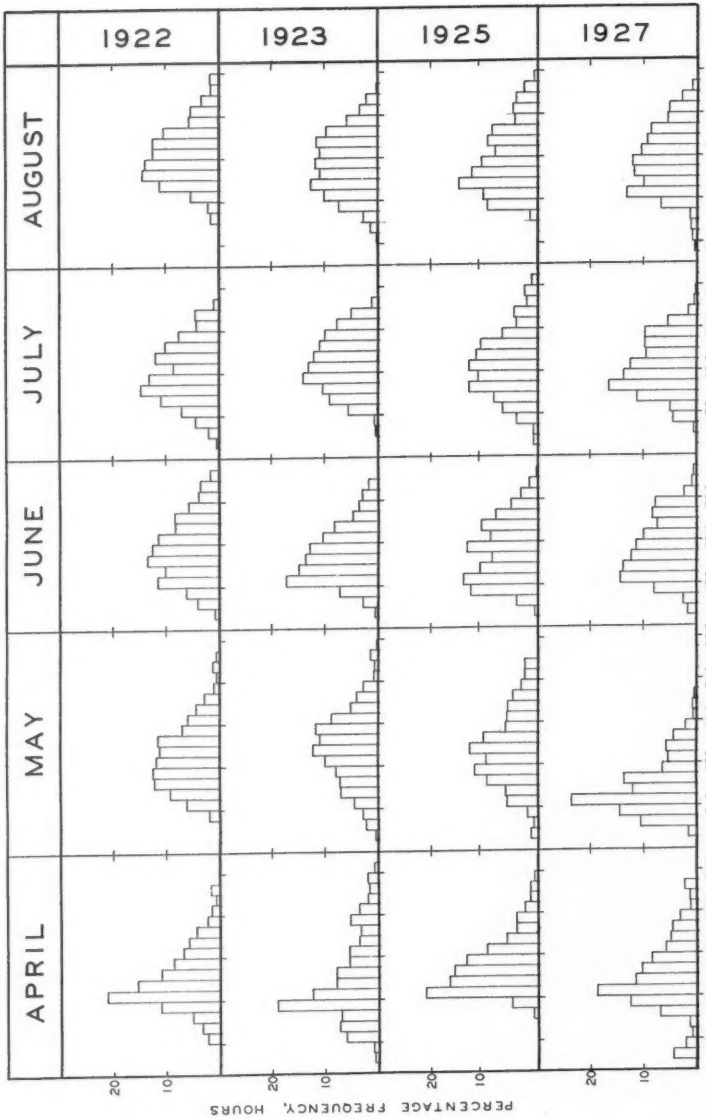


FIG. 9. *Percentage frequency distribution of hourly temperatures at Swift Current, Saskatchewan, during five spring and summer months of 1922, 1923, 1925, and 1927.*

All of the 20 monthly frequency distributions deviate more or less from symmetry, hours with below-average temperatures being in excess of those with above-average ones. The unequal concentration of the hourly values is emphasized in Table XXI, which shows the four quartile ranges, *i.e.*, the

TABLE XXI

QUARTILE RANGES (°F.) OF FREQUENCY DISTRIBUTION OF HOURLY TEMPERATURE OBSERVATIONS AT SWIFT CURRENT

Month	Year	Q_1 (0–25%)	Q_2 (25–50%)	Q_3 (50–75%)	Q_4 (75–100%)
April	1922	15.5–32.4	32.4–37.1	37.1–46.3	46.3–74.5
	23	7.5–29.4	29.4–34.7	34.7–48.5	48.5–81.5
	25	24.5–34.7	34.7–41.3	41.3–48.7	48.7–78.5
	27	7.5–30.6	30.6–36.2	36.2–46.3	46.3–76.5
4 yr. average quartile range		18.0	5.6	10.1	30.3
May	1922	30.5–42.3	42.3–50.0	50.0–59.0	59.0–88.5
	23	21.5–44.7	44.7–54.4	54.4–62.9	62.9–92.5
	25	20.5–43.5	43.5–52.6	52.6–62.8	62.8–87.5
	27	28.5–39.2	39.2–43.5	43.5–51.4	51.4–81.5
4-yr. average quartile range		17.2	7.7	8.9	28.5
June	1922	36.5–52.5	52.5–60.5	60.5–71.1	71.1–91.5
	23	41.5–55.0	55.0–62.0	62.0–69.8	69.8–90.5
	25	38.5–49.6	49.6–59.6	59.6–68.7	68.7–88.5
	27	35.5–51.3	51.3–58.7	58.7–68.1	68.1–89.5
4-yr. average quartile range		14.1	8.1	9.2	20.6
July	1922	37.5–55.6	55.6–62.7	62.7–72.4	72.4–91.5
	23	39.5–59.1	59.1–66.5	66.5–74.9	74.9–91.5
	25	38.5–57.2	57.2–65.0	65.0–73.8	73.8–98.5
	27	40.5–56.6	56.6–63.1	63.1–72.3	72.3–92.5
4-yr. average quartile range		18.1	7.2	9.0	20.1
August	1922	39.5–57.2	57.2–64.2	64.2–72.5	72.5–94.5
	23	34.5–52.7	52.7–60.8	60.8–70.1	70.1–88.5
	25	42.5–52.3	52.3–60.1	60.1–71.2	71.2–94.5
	27	30.5–52.3	52.3–60.7	60.7–70.6	70.6–90.5
4-yr. average quartile range		16.9	7.8	9.6	20.9

temperature intervals comprising 0–25%, 25–50%, 50–75% and 75–100% of the hourly observations for each month each year, and also the average range of each quartile for the four years. This inequality is, like most of the other temperature characteristics dealt with, of a seasonal nature, being most marked in the spring and least pronounced in the summer months. Thus in April the four-year average range below and above the 50% point is 23.6 and 40.4° F. respectively, whereas for July the corresponding figures are 25.3 and 29.1°.

Comparison of 2- and 24-point Daily Means

The hourly records may be further utilized to compare the daily mean temperature, computed in the customary way by averaging the maximum and minimum, with that obtained by averaging the 24 hourly values. In view of the asymmetry of the average diurnal curves, it might be expected that the two means would not in general coincide, and the mean of the daily maximum and minimum (m_2) was in fact found to be on the average in excess of the mean of the 24 hourly observations (m_{24}). The magnitude of the average discrepancy seems to be a function of the season, varying as shown in Table XXII from 1.47° F. in April to a minimum of 0.74° F. in July, in the case of the four-year period studied.

TABLE XXII

Comparison of mean daily maximum and minimum temperature (m_2) and mean of 24 hourly observations (m_{24}) at Swift Current, Saskatchewan, by months

—	April	May	June	July	August
Average difference, $(m_2 - m_{24})$, °F.	1.47	0.94	0.79	0.74	0.83
S.D. of observed differences, °F.	2.1	3.1	2.9	2.7	2.4
Max. diff. in 4-yr. period, °F.	+7.6	+9.1	+9.7	+9.4	+8.0

Although the average discrepancy between m_2 and m_{24} is thus of moderate dimensions, the deviations actually occurring on individual days vary considerably, as is indicated by the standard deviations given in Table XXII, and are sometimes quite large (see bottom line of Table XXII, and also Fig. 10). The source of such fluctuations is of course to be found in the various departures of the individual daily temperature sequences from the average diurnal trend, occasioned by cloudiness, air movements, precipitation, etc. Numerical specification of such departures, and their relation to the deviations of m_2 from m_{24}, has not been undertaken. It has however been noted that there is some correlation between the daily range in temperature and the magnitude of $(m_2 - m_{24})$, such that as the range increases, the excess of m_2 over m_{24} tends to diminish.

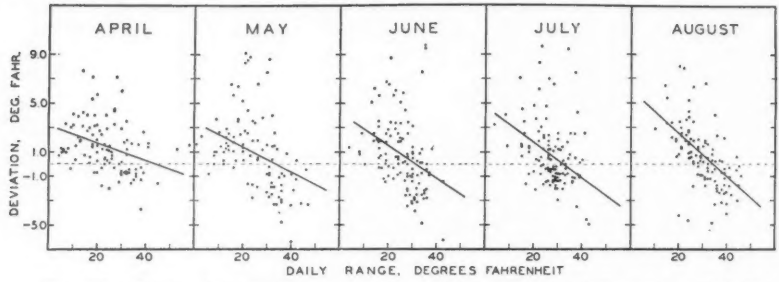


Fig. 10. *Relation between deviation of two-point from 24-point daily mean, and daily range in temperature, at Swift Current, Saskatchewan. Computed from four years' data (1922, 1923, 1925 and 1927).*

Correlation and regression coefficients, calculated from the four years' data, are shown in Table XXIII. The regression coefficients, specifying the average decrement in $(m_2 - m_{24})$ for each increase of 1° F. in the daily

TABLE XXIII

CORRELATION BETWEEN DAILY RANGE IN TEMPERATURE AND DEVIATION OF MEAN OF DAILY MAXIMUM AND MINIMUM FROM MEAN OF 24 HOURLY OBSERVATIONS $(m_2 - m_{24})$ AT SWIFT CURRENT, SASKATCHEWAN, BY MONTHS

——	April	May	June	July	August
Correlation coefficient*	0.32	0.38	0.36	0.39	0.59
Regression coefficient, °F.	−.07	−.10	−.13	−.14	−.18
Residual S.D., °F.	2.0	2.8	2.7	2.5	1.9

**1% point $\leqslant$ 0.25.*

range, increase progressively in absolute magnitude from 0.07° F. in April to 0.18° in August. However, although all five correlation coefficients are statistically significant, the degree of association indicated is only moderate and, as is evident from Fig. 10, accounts for only a minor proportion of the observed variance of $(m_2 - m_{24})$. This is natural, since differences in the daily range reflect only imperfectly the many possible variations in the actual daily temperature sequences. In consequence, it would seem that under the conditions prevailing at Swift Current, the agreement between m_2 and m_{24} may be definitely less satisfactory than is suggested by *e.g.*, the comments of the U.S. meteorologist Kincer (5, p. 5).

References

1. ABBOTT, C. G. The influence of solar variability on weather. Sci. Monthly, 43 : 108-121. 1936.
2. FISHER, R. A. Statistical methods for research workers. (Fifth edition.) Oliver and Boyd, London. 1934.
3. GEIGER, R. Handbuch der Klimatologie, Bd. I, Teil D. Mikroklima und Pflanzenklima. Gebrüder Borntraeger, Berlin. 1930.
4. HOPKINS, J. W. Agricultural meteorology: some characteristics of precipitation in Saskatchewan and Alberta. Can. J. Research, C, 14 : 319-346. 1936.
5. KINCER, J. B. Climate: Temperature, sunshine and wind. (In U.S.D.A. Atlas of American Agriculture). U.S. Govt. Printing Office, Washington. 1928.
6. KINCER, J. B. Is our climate changing? A study of long-time temperature trends. U.S. Monthly Weather Rev. 61 : 251-259. 1933.
7. METEOROLOGICAL SERVICE OF CANADA, DEPT. OF TRANSPORT. Monthly record of meteorological observations in the Dominion of Canada and Newfoundland. Toronto.
8. PEARSON, E. S. A further development of tests for normality. Biometrika, 22 : 239-249. 1930.
9. RAMDAS, L. A., KALAMKAR, R. J. and GADRE, K. M. Agricultural meteorology: Studies in micro-climatology, Part II. Indian J. Agr. Sci. 5 : 1-11. 1935.
10. SELTZER, P. Etudes micrométéorologiques en Alsace. Thèse (D. ès Sc.) Université de Strasbourg. Imprimerie Alsacienne, Strasbourg. 1935.

Canadian Journal of Research

Issued by THE NATIONAL RESEARCH COUNCIL OF CANADA

VOL. 15, SEC. D. OCTOBER, 1937 NUMBER 10

LARVAL AND ADULT STAGES OF BRITISH COLUMBIA ANOMURA[1]

BY JOSEPHINE F. L. HART[2]

Abstract

The external morphology of the adult stage of four species of Anomura (hermit crabs), *Upogebia pugettensis* (Dana), *Paguristes turgidus* (Stimpson), *Pagurus beringanus* (Benedict) and *Orthopagurus schmitti* (Stevens) is compared and the larval stages described. Emphasis is placed on the value of larval stages in clarifying our understanding of the taxonomy and interrelationships of the group. This study seems especially important in the Anomura because of the modifications of the adults which fit them for so specialized a mode of existence. It seems probable that some of the similarities exhibited by them are due more to convergence, as a result of similar mode of life, than to close affinity. This is illustrated by the superficial similarity of the adults of *Paguristes turgidus* and *Pagurus beringanus* and the dissimilarity of their larvae, as contrasted with apparent differences between the adult *Pagurus beringanus* and *Orthopagurus schmitti*, whose larvae are alike. By a comparison of the least modified appendages (the mouth parts) of the adults, the same relationship becomes apparent as was suggested by a study of the larvae. It is therefore concluded that by a comparison of both the larval and adult phases a clearer understanding of the affinities of the species under consideration is obtained.

Introduction

The classification of decapod Crustacea has been long a subject of controversy. One of the chief reasons for dispute is that the animals have been classified almost entirely by a consideration of adult characters. Thus it is to be expected that studies of the larval phases might clarify our understanding of the taxonomy of the group and perhaps suggest relationships not now appreciated. For instance, Lebour (23) has proposed a rearrangement of the classification of the British Brachyura based on a study of the larvae. A study of development would perhaps be even more illuminating in such a group as the Anomura, because of the modifications which fit them for so specialized a mode of existence. It is possible that some of the similarities which the adults exhibit are due to convergence as a result of a similar habit of life. Only ontogenetic studies can conclusively elucidate such a question.

The present study concerns four species of Anomura from British Columbia: *Upogebia pugettensis* (Dana), *Paguristes turgidus* (Stimpson), *Pagurus beringanus* (Benedict) and *Orthopagurus schmitti* (Stevens). The conclusions drawn as to the taxonomy of these forms are based on studies of the developmental stages as well as on the adult characters. Comparatively little

[1] *Manuscript received August 11, 1937.*
Contribution from the Pacific Biological Station, Nanaimo, B.C., and the University of Toronto.

[2] *Temporary Assistant, Pacific Biological Station, Nanaimo, British Columbia.*

information is available on the larval stages of Anomura and none of the forms considered here has been previously described. Except for characters used in identification, the morphology of the adults has received little attention.

Upogebia pugettensis is a symmetrical Thalassinid, not as greatly modified for its burrowing existence as many other members of the group, but with thin integument and lamellate pleopods, which are correlated with this mode of life. The other three species, however, do show modifications correlated with their life in spiral shells or in a straight tube. *Pagurus beringanus* and *Paguristes turgidus* live in gastropod shells and have twisted abdomens and asymmetrical tail-fans, while *Orthopagurus schmitti* lives in a worm tube and shows a lack of bilateral symmetry only in the difference in size of the chelae, and in the distribution of the pleopods. These species were not chosen haphazardly. *Paguristes turgidus* has a number of unusual structures in the adult and its larvae are quite unlike the described larvae of *Pagurus*. *Pagurus beringanus*, on the other hand, is typical in both larval and adult stages, and as its habitat is similar to *Paguristes*, seemed suitable for comparison. The third hermit crab, *Orthopagurus schmitti*, is of interest because of its greater abdominal symmetry and the form of its larvae. *Upogebia pugettensis* was chosen because it lives under somewhat the same conditions as *Orthopagurus* and exhibits a number of apparently primitive characters in all phases.

History of the Study of Classification

The classification of decapod Crustacea has been the subject of much discussion during the last hundred years and continues to be a difficult problem. In 1806, Latreille divided the order Decapoda into Macrura and Brachyura. The division was based on the type of abdomen:— in the first group, well developed and carried straight out behind, and in the second, turned forward under the thorax. This grouping, however, does not hold in the case of some families in which the abdomen is carried in the same manner as in the crabs or Brachyura, but which are obviously more closely allied to the long tailed Macrura. H. Milne-Edwards in 1834 introduced "Anomura", for a group intermediate between the other two and including the higher Macrura and lower Brachyura of Latreille's system. The members of this new group were those which had abdomens somewhat modified from the primitive macrurous type and still showed some remnants of a locomotive function and, with the exception of the Homolidae and Raninidae, retained paired appendages on the sixth segments. These two families are now usually placed in the Brachyura, but because of the type of larvae found in those species whose life history has been investigated, it seems probable that they will soon be moved again from the Brachyura. With the addition of some of the higher Macrura, the Anomura is now considered a natural group. In confirmation of this idea, Gurney (16) has found that the larvae of members of the group have at least one feature in common: the reduction in size of one pair of marginal setae on the telson.

Boas (6) pointed out that the divisions, Macrura, Anomura and Brachyura were not comparable nor were they of the same status taxonomically. His contention was that the Macrura consisted of a great variety of forms, some of which were more closely allied to members of the Brachyura or of the Anomura than they were to other members of their group. He therefore divided the order into the suborders Natantia or swimming forms, comprising the freely swimming shrimps, and the suborder Reptantia or creeping forms, including the Brachyura, the Anomura, the Thalassinidea, the Astacura, the Palinura and the deep-sea Eryonidea. Borradaile (10) adopted the main points of Boas' classification. His (9) most important change in this connection was the inclusion of the Thalassinidea (sand shrimps) with the tribe Anomura (hermit crabs), because of their resemblances to the primitive symmetrical hermit crabs. According to Borradaile, the only constant important differences are the presence in the latter of a pleurobranch on the last pereiopod, a suture across the telson, no epipodites on the legs, a reduced rostrum, subchelate fourth legs, and narrow uropods.

Benedict (3, 4) revised the nomenclature of the genera of the Paguridae and replaced *Eupagurus* with *Pagurus* and suggested *Pagurias* for those Pagurids described during the nineteenth century as *Pagurus*. These changes do not seem to have been universally adopted, but as recent American authors have used them in the revised form, *Pagurus* in this paper refers to those formerly called *Eupagurus*. This use, however, makes the names Pagurinae and Eupagurinae given in Borradaile's (10) classification untenable and therefore the subfamilies are referred to here as I and II.

Class *CRUSTACEA*

Order DECAPODA.

Suborder *Reptantia.*

Tribe Anomura.

Superfamily Thalassinidea

Family Callianassidae

Subfamily Upogebiinae

Upogebia pugettensis (Dana)

Superfamily Paguridea

Family Paguridae

Subfamily I

Paguristes turgidus (Stimpson)

Subfamily II

Pagurus beringanus (Benedict)

Orthopagurus schmitti (Stevens)

Food

The feeding habits of all the species concerned in this paper are somewhat similar. McGinitie (26) says that *Upogebia pugettensis* feeds on detritus, which is caught by means of the "basket" formed by long hairs on the first two pairs of pereiopods through which water, containing particles of plant and animal remains, is forced by the action of the pleopods. The detritus is then cleaned off the "basket" with the third maxillipeds and conveyed by the other appendages to the mouth. If large particles of food are introduced, they are rejected by the animal.

No work has been done on the feeding habits of the hermit crabs of British Columbia, but as the habitat and modifications of the mouth parts are similar to those species that have been studied, it would seem safe to assume that they are alike in this respect. Orton (34, p. 920) states "*E. bernhardus* obtains food largely by its small claw and third maxillipeds, and may at certain periods of the year feed mainly on micro-organisms, and at others on macroscopic, but mainly tiny living organisms which have been disturbed and captured in the deposits on the sea bottom. Food can be obtained by the use of the third maxillipeds alone. The mouth parts of *E. bernhardus* are not adapted for rapid ingestion of the meats of animals in bulk, and the gastric mill is less strongly developed than in the carnivorous crabs: these facts, along with certain features of the gut, indicate morphological and anatomical modification correlated with the food and mode of feeding."

Orthopagurus schmitti, owing to its enforced stationary existence, is a plankton feeder, catching the organisms in the water by means of the action of its third maxillipeds, which are fringed with stiff bristles. The mandibles of all these species are comparatively feeble, indicating that the food does not require much mastication.

Material

The study of decapod Crustacea, on which the present paper is based, was commenced in the summer of 1928, when a collection of shore species was made in the vicinity of Victoria, British Columbia. The results of the study of this collection, together with some additional specimens obtained the following summer at Nanaimo, were published in 1930 (18). Specimens of adult Anomura, obtained while the writer was working at the Pacific Biological Station, Nanaimo, from 1929 to 1934, have been augmented by specimens from Victoria, and from points on the west coast of Vancouver Island, collected by Mr. E. G. Hart in 1934. Thus a considerable number of individuals of the species dealt with here were available for study.

Records of *Orthopagurus schmitti* have been published only by Stevens (40, 41), who described the species from Friday Harbor, Washington, and by the writer (18) from Nanaimo. *Upogebia pugettensis* is the only one of the species dealt with in which the morphology has been investigated except for those features used in the classification. The descriptions of the structure of the other three species are therefore given here for the first time.

Knowledge of the life history of decapods is scanty, especially concerning species from the Pacific coast of North America. From this area Berkeley (5) has published descriptions of some of the larval stages of five pandalid shrimps, and of five Hippolytidae (Berkeley (5) Needler (31)). Marukawa (27) described the larvae of the Anomuran King crab, *Paralithodes camtschatica* (Tilesius). All the larval stages of four species of true crabs were reared from the egg, and described by the writer (19). Thus the Anomuran larvae of British Columbia, with the exception cited above, are unknown.

The experimental rearing of Brachyura and Anomura was therefore started during the summer of 1930 (May until August) and continued during the same period of 1931, from January until July in 1933 and during July and August, 1934. Three species of hermit crabs were reared from the egg to the adolescent stages during 1931 and 1934 by the writer. In addition to these complete series, more than two dozen incomplete life histories, comprising about 75 post-embryonic stages, have been obtained by rearing from the egg. The culture methods have been described briefly (20, 21).

One soon becomes familiar with the characters of various groups and even of some of the genera, so that the stages can be readily distinguished in the plankton. The larval stages of allied forms are often very similar, and specific differences are difficult to determine. In a genus such as *Pagurus*, with some 15 species in British Columbia, careful and detailed comparison of the larvae is necessary, in order to determine specific features with any degree of certainty, and rearing from the egg is essential. The spawning season of most species is prolonged, so that the number of species to be found in the plankton at any time is great. The larvae are usually distinctively colored, but as all color is lost in preserving them, morphological differences must be relied upon. In the Anomura, the characters showing the greatest variation among species, and yet the least modification during the development and growth of the individual, are the carapace, the abdomen, the antennae and the telson.

Morphology of Adults

Upogebia pugettensis (Dana)

Upogebia pugettensis (Dana), the so-called mud-shrimp, is the first species dealt with here. There has been considerable controversy in the past about the position in the system of classification of the group to which this species belongs. The Thalassinidea are shrimp-like burrowing Reptantia. Correlated with their mode of life are certain modifications, such as a reduction in the number of gills, softening of the integument of the abdomen, and reduction in size of the pleura. It would seem probable that some of the characters in common within the group are due to convergence and not to close phylogenetic relationship. The Thalassinidea resemble the hermit crabs in some respects and the lobsters in others. Features common to both Thalassinidea and the lobsters, are the shape of the tail-fan, of the first leg

and often of the second. They resemble the hermit crabs in the mode of concealment, in the thorn-like shape of the antennal scale (where this structure is present in the adult), in the freedom of the last thoracic sternite and the mode of carrying the last pair of legs. In view of these features, Borradaile (8) and Calman (12) put the family in the tribe Anomura, while Ortmann (32) and Bouvier (11) consider them to be more closely allied to the lobsters. Gurney (16), from a study of the larvae, feels that the resemblances to the Anomura are greater in this phase. He also points out that the Thalassinidea is not a homogeneous group, and that with further knowledge it will be split into at least two series. We are, however, concerned here only with one species of the subfamily Upogebiinae and its resemblance to the hermit crabs, and in this connection the Anomuran affinities are of greatest interest.

Stevens (42) has ably described and figured this species and made ecological notes. The ecology has also been studied by McGinitie (26). The papers of these two writers have been most useful in the discussion and comparison of the species dealt with in this paper.

It will perhaps suffice to mention that *Upogebia pugettensis* (Dana) is macrurous in shape, often reaching 90 mm. in length of body, and dwells in burrows, about 25 mm. in diameter, tunnelled in sandy mud or gravel by means of the animal's walking legs and tail-fan. The species occurs commonly on tide flats from Southern Alaska to Lower California.

Paguristes turgidus (Stimpson)

Paguristes turgidus (Stimpson) is a hermit crab inhabiting fairly deep water (to 254 fathoms) from British Columbia to Southern California. It usually occurs on a rocky bottom and in considerable abundance. The shell commonly occupied is the moon shell, *Polinices*, and there is a tendency for the individual to choose a shell larger than necessary, so that it can withdraw itself completely within its shell and can be reached only by breaking the shell. Although this is the only species of the genus recorded from British Columbia, other species are found in California and in nearly all tropical and semi-tropical regions.

P. turgidus may have a carapace of about 25 mm. in length, with a total body length of 75 mm. It is an interesting form because the chelae are subequal, the left being the larger; paired appendages in addition to the uropods are present on the abdomen and there is an egg pouch in the female. The animal is in general a deep red, toned down in color by tan hirsuteness and the brown bases of spines. The antennules and eyestalks are striped longitudinally with red and white. The abdomen is yellow, except in the mature female, where the ova show scarlet through the thin integument. The pleopods are pink and the uropods red with yellow setae.

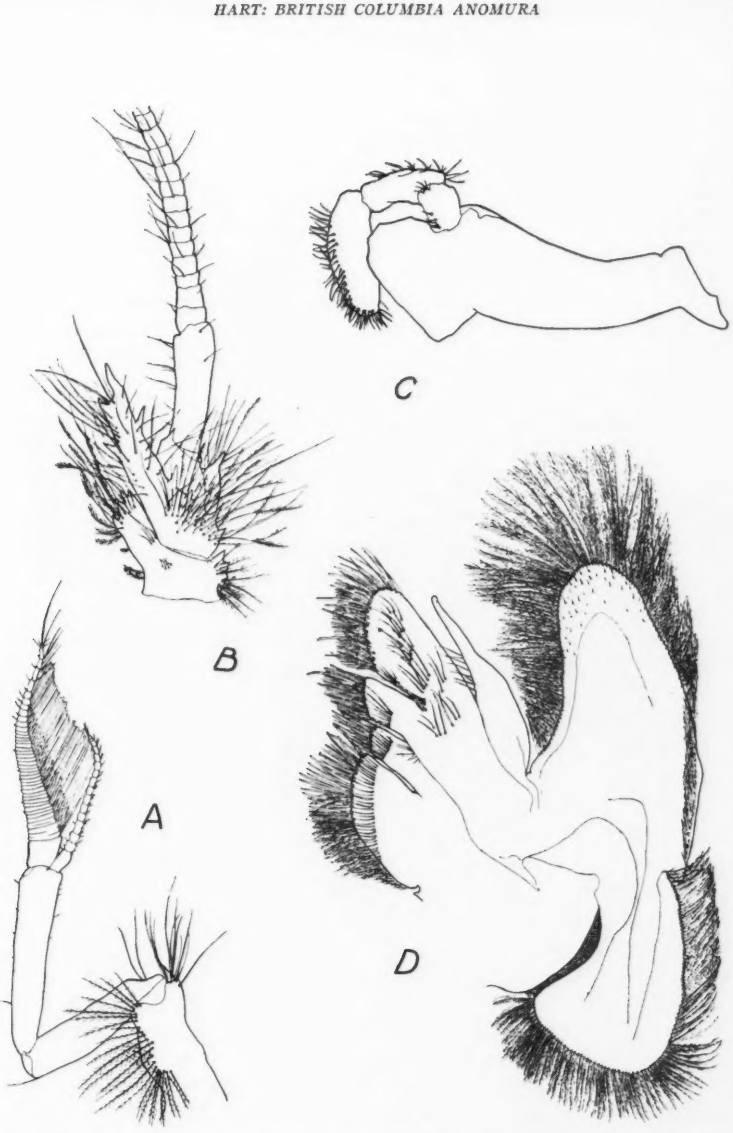


FIG. 1. *Paguristes turgidus (Stimpson). Male. A. Antennule. B. Antenna. C. Mandible. D. Maxilla.*

Female (Plate I, Fig. 1; Fig. 3, A-C)

Paguristes turgidus (Plate I, Fig. 1) is a stout species: hairy, and with dark-tipped spines on the subequal chelae and walking legs. Most of the hairs are plumose. Carapace thinly calcified, especially the posterior part. Rostrum and lateral spines subequal: small and sharp-pointed. Abdomen large, dextrally twisted, with tergum and sternum of first segment calcified; as is area around pleopods on left side and corresponding region of right side, of second to fifth segments. Sixth segment and telson also calcified. Some indication of calcification along ventral margin of outgrowth (which serves as a partial egg pouch) found on posterior part of fourth segment on left side. Telson (Fig. 3, A) asymmetrical, left side much larger than right, with sutures cutting off triangular postero-lateral portions: posterior margins toothed. Eyestalks long, cylindrical, and scales cut into a number of deep teeth.

Antennule rather flattened laterally; the first segment of peduncle with three large spines, the second and third segments narrower than first. Inner flagellum large, multiarticulate, and nearly twice as long as narrow outer flagellum. Antenna has short coxopodite; basipodite armed with a large spinous protuberance, about half the size of spined scale (exopodite): first segment of endopodite has a large spine, second a smaller one and third smooth and equal to sum of lengths of other two; flagellum comparatively short; stout and hairy.

Right mandible with a somewhat triangular incisor and a rounded molar; small basipodite; first segment of endopodite with a few setae and second with numerous bristles. Left mandible similar, except that cutting surface is rounded, with a few flat teeth.

Maxillule with endite of coxopodite broad and that of basipodite narrower and longer: endopodite rather large, with bristles on tip and large lateral and posterior extension (second segment); exite (epipodite ?) large. Maxilla has large endites, heavily bristled: a fair-sized endopodite, tapering towards tip, with sparse lateral bristles; scaphognathite large with dense brush of setae on margin, and a fold indicating fusion of exopodite and epipodite.

First maxilliped with a thick triangular coxopodite, and a flat basipodite produced distally, with stout bristles on inner margin. Endopodite composed of a single curved segment; proximal portion of exopodite swollen, heavily armed with hairs, and bearing a narrow segment with flagellum of a few poorly defined segments: and epipodite large and lying against exopodite. Second maxilliped of usual type, with endopodite of five segments and a well developed exopodite with flagellum. Third maxilliped stout with bases of appendage closely approximated: endopodite armed with a row of heavy spines on ventro-medial margin of merus, other segments with stiff bristles; exopodite large and flagellate. Two arthrobranchs: phyllobranchiate with rather elongated leaves.

First pereiopod chelate, left subequal to right; rather short, stout and heavily armed with spines and plumose hairs, except on medial surface and

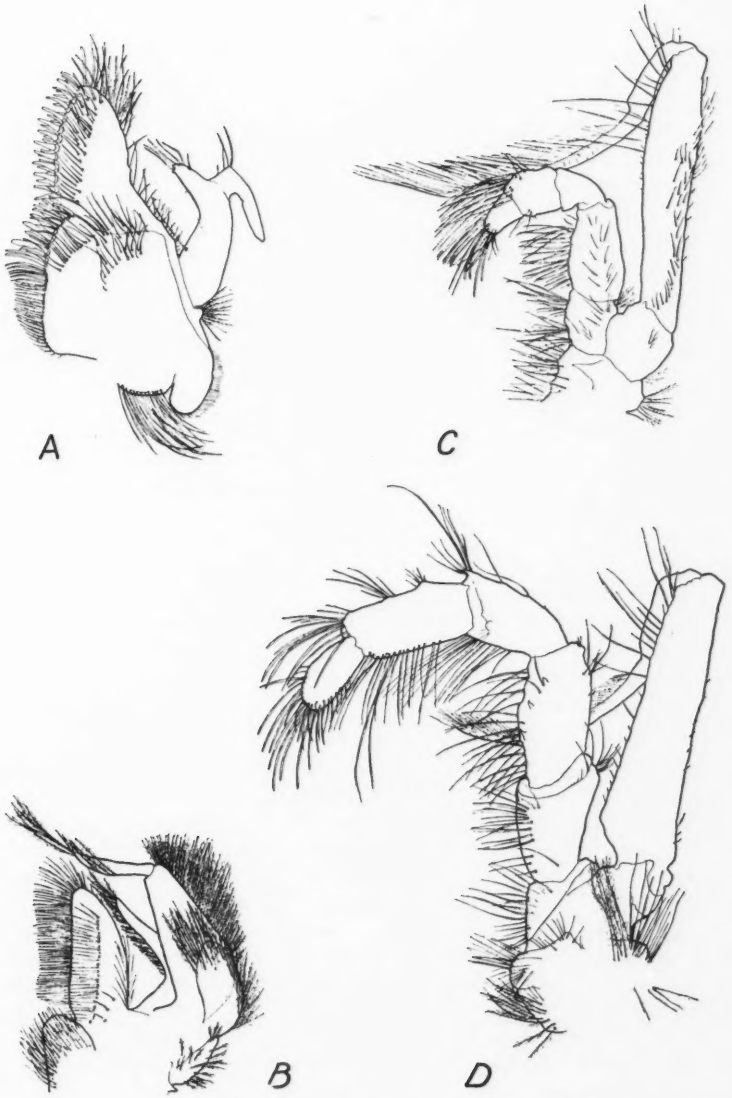


FIG. 2. *Paguristes turgidus (Stimpson). Male. A. Maxillule. B. First maxilliped. C. Second maxilliped. D. Third maxilliped.*

outer side of merus; tips of chela strongly sclerotized. Two arthrobranchs. Second and third pereiopods well developed, elongated and armed with spines and plumose hairs. Each has two arthrobranchs and one pleurobranch. Fourth pereiopod small, with long hairs and suctorial setae on distal ventral surface of propodus. It is simple, not subchelate. Two arthrobranchs and one pleurobranch. Fifth pereiopod, which is carried folded up posterior and dorsal to carapace, also small, with bunches of hairs and definitely chelate (broad flat thumb and movable finger) with suctorial setae. No gills.

First pleopod (Fig. 3, B) small, with fused joint. Distal part probably endopoditic in origin, because in *Upogebia* a similar pleopod carries eggs, and these are borne only by endopodites. Few marginal setae. Second pleopod (Fig. 3, C), as well as third, fourth, and fifth, borne only on left side. Second made up of protopodite, rather broad distally, and subequal endopodite and exopodite. Third similar, except that exopodite larger than endopodite. Fourth has an even larger exopodite than third. Fifth pleopod has no endopodite, but exopodite well developed. Uropods or appendages of sixth segment (Fig. 3, A) unequal in size: that of the left side much larger than right, and both with exopodites larger than endopodites. The flattened posterior surfaces bear numerous suctorial setae.

Male (Plate I, Fig. 2; Fig. 1; Fig. 2; Fig. 3, D-E)

Male of *Paguristes turgidus* (Pl. I, Fig. 2) differs from female mainly in armature of abdomen and its appendages. Abdomen of male more strongly calcified than that of female. First segment is similar to that of female. Tergum and part of sternum of second calcified, as is a large part of tergum of third segment, which is armed with soft hairs posteriorly. Fourth and fifth like third, but to a lesser degree, while sixth has tergum strongly calcified.

Paired abdominal appendages of first and second segments highly specialized for transference of spermatophores to body of female. Paired appendages (Fig. 3, D) of first segment lie fairly close together; each is a short, stout, uniramous limb of two segments. Protopodite margined on inner edge with stout setae and endopodite(?) hollowed out, twisted and armed with stout bristles and teeth to form upper half of tube. Second pair of pleopods (Fig. 3, E) longer and their bases farther apart with protopodite unarmed and distal half of endopodite(?) grooved to fit over that of first appendage. Second pair of pleopods covered with coarse bristles distally. Remaining pleopods (present on left side only) all lack endopodites (with one exception, a small endopodite on third pleopod of large male figured). In lacking endopodites, male differs from female of species and from males of *Pagurus* and *Orthopagurus*. Pleopods of third and fifth segments subequal in length and that of fourth somewhat longer. They all bear tufts of setae on protopodite, and exopodites are margined with numerous long plumose setae.

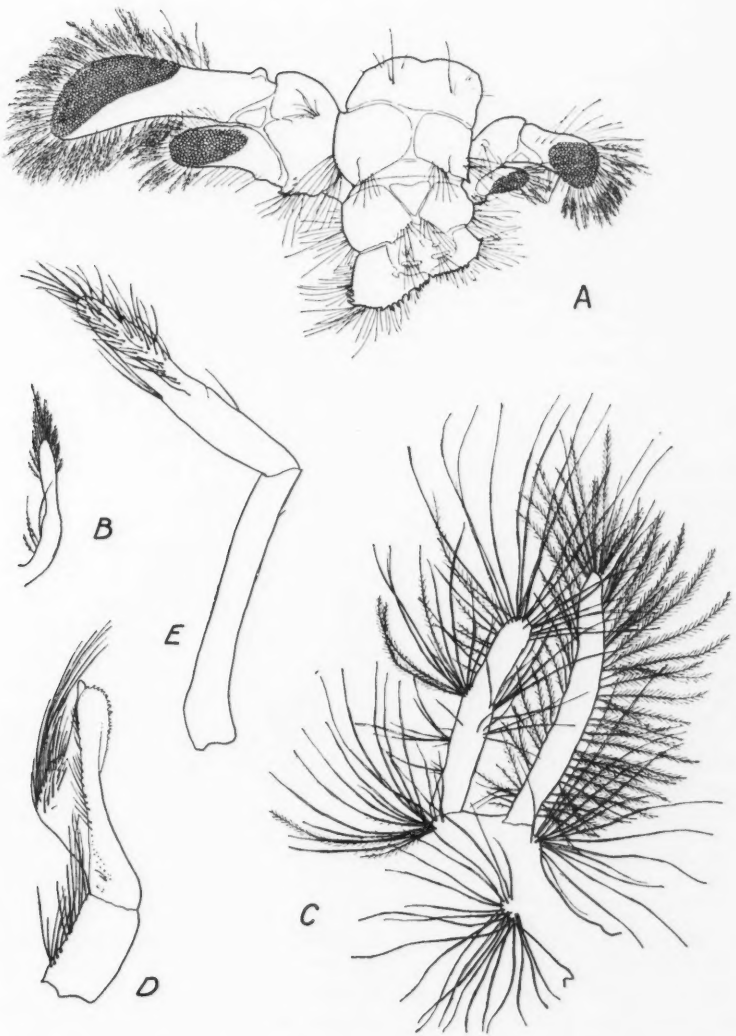


FIG. 3. *Paguristes turgidus (Stimpson). A-C, Female. A. Telson and uropods. B. First pleopod. C. Second pleopod. D, E, Male. D. First pleopod. E. Second pleopod.*

Pagurus beringanus (Benedict)

Pagurus beringanus (Benedict) is a typical hermit crab, with large right claw and asymmetrical abdomen with paired appendages on the sixth segment only. In the Nanaimo region, *P. beringanus* is commonly taken with *Paguristes turgidus*, and for this reason is used here. It is, however, a shallow water species, not having yet been obtained from water more than 40 fathoms deep. In the Nanaimo area, the adults are not found near the shore at low tide, but they are common on all rocky shores in the Straits of Juan de Fuca. The lower temperature of the water in the latter area may account for this difference in distribution.

P. beringanus usually occupies the empty shells of the whelk, *Thais* and, like Paguristes, chooses large ones. Frequently there is a break in the shell near the tip, and a small individual of the same species lives in the upper part, with a large one in the lower. The coloring is brilliant: gray-green chelipeds, except for a white band near the tips, with orange granules and spines; the pereiopods green and white, spotted with rust, which is concentrated into a band at each joint; and the remainder of the body flecked with scarlet and brown; mainly scarlet on the branchial region of the carapace and on the abdomen. The eyestalks and antennae are brown.

Female (Plate I, Fig. 3; Fig. 4, A-C)

Pagurus beringanus (Plate I, Fig. 3) is quite a stout species, with a fair number of fine hairs (none plumose). Chelipeds armed with short spines and spiny granules. Carapace may reach a length of 20 mm. and body about 50 mm. Carapace fairly well calcified anteriorly, but thin and soft posteriorly. Rostrum and lateral teeth very obtuse. Abdomen with calcified area on tergum of first segment; two lateral, elongated patches on second and third segments, and small round areas on fourth and fifth. No brood pouch. Sixth segment and telson (Fig. 4, A) similar to those of *Paguristes turgidus*. Eyestalks long, but scale small and triangular and not cut into teeth.

Antennule like that of *Paguristes* except that there are two rows of long bristles instead of scattered short setae on inner flagellum. Antenna is a narrower appendage with spines on basipodite, with a narrow sickle-shaped exopodite and a longer flagellum, with very short bristles between articulations.

Mandibles each have three blunt teeth and the separation between basipodite and endopodite is not clearly defined. Endites of maxillule not as well developed as those of *Paguristes;* endopodite differs in having only one bristle on inner side of flattened apex and a small knob on outer corner. Exite much smaller. Maxilla very like that of *Paguristes* except that there are bristles at tip of endopodite, and no suture which might indicate that the scaphognathite is made up of two parts, as is seen in the other form.

First maxilliped (Fig. 4, C) much smaller and less twisted than that of *Paguristes*. No epipodite. Second maxilliped similar in the two forms but

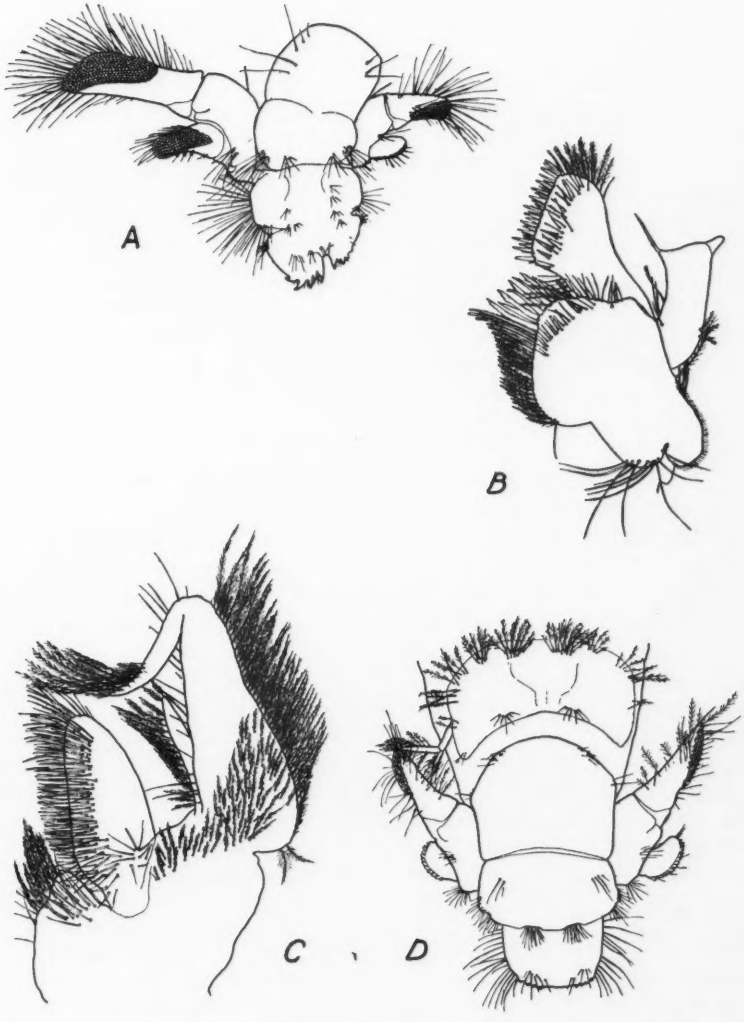


FIG. 4. *Pagurus beringanus (Benedict). A-C, Female. A. Telson and uropods. B. Maxillule. C. First maxilliped. D. Orthopagurus schmitti (Stevens). Male. Telson and uropods.*

flagellum slightly shorter. Third maxilliped is smaller than that of *Paguristes*, but like that species has a row of teeth on inner edge of ischium, and there are a larger number of comb setae on dactylus and propodus, in fact the whole endopodite is more densely armed with bristles. Coxae separated. Two arthrobranchs on each appendage.

Right cheliped much larger than left, and both with rather short thumbs and fixed fingers. Two large tubercles present on ventro-distal part of merus of right one. Two arthrobranchs. Next two pereiopods long, with no pleurobranchs. Fourth very small, about $\frac{2}{3}$ that of *Paguristes*, subchelate with tuberculate edge on short propodus. Two arthrobranchs and one pleurobranch. Fifth leg also small, chelate, although not as clearly so as in *Paguristes*.

No pleopods on first segment of abdomen; and those of second, third and fourth segments differ from *Paguristes*, in that the bases of exopodite and endopodite are close together, and the end of protopodite narrow. The two parts are more nearly equal in size. Fifth pleopod has a short endopodite. Uropods similar to those of *Paguristes*.

Male

Integument of abdomen of male is like that of female in degree of calcification. No pleopods on either side of first and second segments, and only on left side of third, fourth and fifth. Pleopods have a large exopodite and a small endopodite.

Orthopagurus schmitti (Stevens)

Orthopagurus schmitti (Stevens) is a small hermit crab (up to 40 mm. in length) inhabiting empty worm tubes of two species of *Serpula* and of *Sabellaria cementarium* Moore. The species is of interest here because the abdomen is straight, not coiled as in *Pagurus* and *Paguristes*, and the telson and uropods are symmetrical, but the other abdominal appendages are on the left side only as in *Pagurus*. It occurs in shallow water (to a depth of about 100 fathoms) and is obtained by dredging up the rocks to which the worm tubes are attached. At minus tides, some of these rocks are exposed at Horswell point, but in other places dredging is necessary. It is quite common locally, but has been recorded only from the Friday Harbor and Nanaimo regions.

O. schmitti is somewhat pubescent, with brown hairs. The coloring is bright: pink or white with orange-brown bands and patches.

Female and Male (Plate I, Fig. 4; Fig. 4, D)

Carapace with a hard smooth cephalic portion, and the remainder very lightly calcified. Rostrum of a fair size, but lateral teeth small. Eyestalks fairly stout, pear-shaped, and a small triangular scale. First segment of abdomen calcified, as are small patches on either side of dorsal part of second, third and fourth segments. No columellar prominence. Fifth segment with part of tergum calcified, showing indication of an overlapping fold posteriorly and apparently used to assist in retaining a hold in tube. Sixth

segment of abdomen (Fig. 4, D) with tergum well calcified and divided very definitely by a deep groove. Telson (Fig. 4, D) quite symmetrical, with rounded lateral margins and a few shallow teeth on posterior straight margin.

Antennule like that of *Paguristes turgidus* except that there are no bristles on peduncle. Antenna like that of *Pagurus*, except that setae between articulations of flagellum longer, but shorter proportionately than those of *Paguristes*.

Mandibles, maxillae, maxillipeds and first three pairs of pereiopods resemble those of *Pagurus beringanus*. Fourth pereiopod smaller than fifth, subchelate and flattened distally. Fifth does not reach carpus of third, and is chelate. Pleopods present on left side of second to fifth segments. Endopodite and exopodite subequal except for fifth, where endopodite small; protopodite narrow. Uropods (Fig. 4, D) subequal and similar, with large exopodite and small endopodite.

Pleopods of male present only on third to fifth segments.

Comparative Morphology of the Genera

The problem is to determine those characters which are not the results of modifications due to a similar mode of life (convergence) but which remain comparatively unaffected by a change of habitat and also to find those that are vestigial.

The four species dealt with here have a somewhat comparable habitat and they exhibit certain modifications in common. They all live protected by substances not secreted by themselves, *i.e.*, hollow objects: *Upogebia* in its sand burrow, *Paguristes* and *Pagurus* in gastropod shells and *Orthopagurus* in calcareous or stony worm tubes. Thin integument is found in each, especially on the carapace and abdomen. This seems to be a character associated with life in a protected spot.

Paguristes resembles *Upogebia* in the adult phase in a number of morphological characters. The rostrum of both species is small and the surface of the carapace posterior to it, roughened. In *Upogebia*, according to McGinitie (26), this serves to hold the animal in position against the top of the burrow while the pleopods fan the water for food and for aeration. In *Paguristes*, it probably assists the animal to retain a hold in its shell and to resist efforts to dislodge it. The flagella of both species are rather short and hairy and although the adult *Upogebia* has but a vestigial scale on the antenna, some allied forms have it well developed. The endopodites of the maxillules are two-jointed and the exite (epipodite?) large. There are indications that the scaphognathite of the maxilla of both species is made up of two parts (exopodite and epipodite). The bases of the third maxillipeds are approximated. The first pair of pereiopods are alike (chelate) and subequal; the fourth pair are simple (neither chelate nor subchelate) and the fifth is chelate in *Paguristes* and often in *Upogebia*. In the females of both

species, the pleopods of the first segment are small, paired and uniramous. The males have paired pleopods on the second segment, but these are modified for copulation in *Paguristes* only. The pleopods in *Upogebia* serve as a means of creating a powerful current of water through the burrow and incidentally drawing in a supply of food, while those of *Paguristes* need only occasionally stir the water within the shell. The females of both species carry the eggs on the setae of the endopodites.

In all these characters except the last, *Paguristes* differs from *Pagurus* and *Orthopagurus*, but resembles them in its mode of life and many of the modifications that fit it for such an existence, particularly the general body shape. The symmetry or lack of symmetry of the appendages does not coincide in the three species.

The carapace of *Paguristes* has the same general shape as that of *Pagurus*, but the distribution of the hard parts (calcified chitin) and of the grooves is different. The abdomen is twisted like that of *Pagurus* (of the same habitat), but shows more vestiges of segmentation. It differs, as does *Pagurus* in this feature, from *Orthopagurus*, which has a symmetrical abdomen suited for life in straight tubes. The antennules, antennal scale, mandibles and second and third maxillipeds, are similar in the three species, but are of the unspecialized decapod type, with the exception of the antennules, which are more like those of the Brachyura, than the more primitive type found in *Upogebia*. The first pereiopod is so twisted that the chelae open horizontally and the axis of the joint between the carpus and propodus is such that an "operculum" may be formed by the chelae, thus preventing intruders from entering. *Upogebia* uses the tail-fan for blocking the entrance to its burrow. The fourth and fifth legs are reduced in size, but as there is a tendency in all Anomura for the differentiation of the fifth legs, and their specialization for cleansing purposes, only the reduction in size of the fourth legs is of interest here. In *Pagurus* and *Orthopagurus* this reduction is greater than in *Paguristes* (30% and 40% of the third legs). *Paguristes* resembles *Pagurus* and *Orthopagurus* in the absence of pleopods on the right side of the second to the fifth segments of the female and of the third to the fifth of the male. The telson and uropods are asymmetrical in *Paguristes* and *Pagurus*, but not in *Orthopagurus*.

Unique Features

Paguristes turgidus differs from *Upogebia*, *Pagurus* and *Orthopagurus* in several important characters:

1. The grooves of the carapace.

2. The presence of a greater number of gills. There are ten arthrobranchs and three pleurobranchs on each side, as compared with ten arthrobranchs only in *Upogebia*, and ten arthrobranchs and one pleurobranch in *Pagurus* and *Orthopagurus*.

3. The presence of paired appendages specialized for copulation on the first and second segments of the abdomen of the male.

4. The presence of an outgrowth or egg pouch on the left side of the fourth segment of the abdomen of the female. This structure is found only in one other genus, *Paguropsis*, which according to Alcock (1) is closely allied to *Paguristes*, and differs only in having a straight abdomen, symmetrical telson and uropods, cheliform fourth legs and unpaired appendages and egg pouch indifferently on the right or left side of the abdomen.

Orthopagurus schmitti differs from the other three species in the partial restoration of the tergum of the fifth segment of the abdomen and in the symmetrical uropods adapted for holding the body within a hollow worm tube.

History of the Study of Development

Until about a hundred years ago it was believed that all decapod crustacea developed directly, in other words, with no metamorphosis. When Thompson (43) hatched the eggs of *Cancer pagurus* and obtained the zoeae, his report on these findings was not credited by many of the scientific men of the times. Westwood insisted that "no exception occurs to the general law of development in the Crustacea; namely that they undergo no change of form sufficiently marked to warrant the application to them of the term metamorphosis" (2, p. xliii). This idea was deeply implanted in the minds of contemporary workers largely because of the extensive work of Rathke on the development of the river crayfish, *Astacus fluviatilis*, in which, because of the life of the adult, planktonic larval stages would not be feasible. The confusion at this time was increased by observation of female crab abdomens from the tropics, to which fully developed and recently hatched young were attached. These were believed to be land crabs (13) which naturally would be governed by the same restrictions as the crayfish.

Thompson (44) described the larvae of 15 decapods including *Pagurus*. The post-larval hermit crabs were first described as adult animals under the generic name of Glaucothoë. Müller (30) surmised their true relationship to the adults.

Culture Methods

General methods for culturing both adult and larval Anomura have been given previously (20, 21). Therefore only a few additional notes are added here.

The study of the larval development of any marine form is fraught with difficulties, which are augmented in a locality where the life histories of few of the species have been worked out. Bovard and Osterid (7) published a list of those animals from which embryological material may be obtained during the months of June, July and August at Friday Harbor, Washington. This list is useful for work in the immediate vicinity of Victoria but is quite misleading for the Nanaimo district. In the latter region, although it is nearly 100 miles north of Friday Harbor, or Victoria, hydrographical conditions are more temperate, and many species spawn weeks, or even months, earlier in the season.

Few papers give any information on the spawning of Pacific coast decapods, but some record ovigerous females, and this information is sometimes of value in the case of forms that do not carry their eggs for a long period, and those that have a definite spawning season. The recording of "ovigerous" females does not take into account the degree of development of the eggs. It has thus been necessary for the present author to make her own records of the egg-carrying and of the spawning periods of the hermit crabs of British Columbia. The approximate state of development of the eggs has also been kept.

The period of incubation of the eggs differs greatly, but seems to vary in most cases directly with the size of the adult. It was found difficult to keep berried females of *Upogebia pugettensis* alive in aquaria, and thus to determine approximately the length of time the eggs are carried. McGinitie (26) found it necessary to provide the "shrimps" with tubes to live in. It is also difficult to induce *Paguristes turgidus* to hatch its eggs in the laboratory. The female will cast off a few eggs each day so that unless they are nearly ready to hatch when obtained, they will all be shed before hatching time. If a few still remain, they are generally delicate and die without casting the prezoeal cuticle.

A minimum of exposure to light seems to be preferred by most, but except for direct sunlight, fairly bright light does not appear to be especially detrimental. They are, however, more active at night, and usually the eggs hatch at this time. As low a temperature as is practicable is advisable (15–20° C.), but the majority seem able to withstand a surprising range.

Hermit crabs as a whole do not thrive without shells and as it is necessary to be able to observe the state of the eggs from time to time, the most satisfactory method is to break a window in the shell, through which the eggs may be seen, even though the animal has retired into her shell.

The egg yolk of *Upogebia* and thus the egg mass, is a bright yellow when freshly extruded, but with the absorption of the yolk and the development of the eye pigment, the mass changes to a brownish color. The egg mass of *Paguristes turgidus* is at first a bright coral-red, changing with development to yellow. The egg mass of *Pagurus beringanus* changes from brownish black to gray. The eggs of *Orthopagurus schmitti* have not yet been seen.

In the jars containing larvae, the prevention of too abundant growth of diatoms and protozoa was accomplished by moving all the larvae, by means of a large-bore pipette, as frequently as necessary to a fresh jar of sea water and food material. The sea water used was not filtered, but care was taken not to include such forms as amphipods and jellyfish, as these will clean out a jar of larvae in an extremely short time. Unless the inner surfaces of the jars were cleaned carefully, worms and barnacles were found to have settled down and grown large enough to be a menace to the larvae.

The rearing of the larvae of hermit crabs is a long and tedious process, and the mortality is extremely high. Only by repeated attempts and by

the use of a large number of individuals, may a few be brought beyond the early stages. Failure has been complete and consistent in many species, the larvae never becoming robust enough to cast off the last embryonic cuticle. However, if sufficient berried females are available, the first larval stage may be obtained occasionally, but the emergence of second stage larvae from first is the crucial point. The post-larvae are comparatively easy to keep if they are healthy when they reach this stage. The adolescent stages of those forms that will eat minced clam muscle thrive as long as they are not crowded or underfed, under which circumstances cannibalism occurs.

Larval Development

Subfamily Upogebiinae

The larval stages of European species of *Upogebia* and *Gebiopsis* have been described by various authors. Sars (38) studied a Norwegian form, Cano (14) a Mediterranean, and Webb (46) the British species. Doubt has been expressed as to the correctness of identification of these species, but since the larvae are certainly the young of these closely allied genera, the exact species is quite immaterial for comparison with the larvae of *Upogebia pugettensis* (Dana), which is found only on the Pacific coast of North America. Gurney (16) and Menon (28) have described larvae from the plankton of New Zealand and Indian waters. *U. danai* from New Zealand and *U. pugettensis* are quite similar, while the *Upogebia* (?) sp. from India shows interesting intergradations between *Upogebia* and *Paguristes* in the larval stages, a subject which will be dealt with later. Gurney (17) describes a *Upogebia* from the Red Sea in which there is no metamorphosis; the first free living form resembles the post-larva of other species.

Gurney (16) gives the characters which distinguish the larvae of Upogebiinae and with these *U. pugettensis* agrees, except for one character, namely, the presence of a distinct unarmed palp on the mandible of the second and third larval stages. The first larval stage of this species is somewhat more advanced than *U. danai* as the pleopods are quite elongate, and can hardly be described as "minute knobs", as in the latter. The second stage is similar in having six pairs of thoracic appendages with functional exopodites, but differs by the presence of a mandibular palp. The third stage also differs from that of *U. danai* and the European forms, in the shape of the telson, which is more triangular and has the posterior margin sloping slightly inwards from the lateral to the median spines. The fourth pair of spines are not strongly developed and those lateral to these are on a level with them, not on a sloping margin. There is no lateral spine on the exopodite of the uropod as is seen in other described *Upogebia*.

Upogebia pugettensis (Dana) (Figs. 5 and 6)

At Friday Harbor, Washington, females of *Upogebia pugettensis* (Dana), bearing eggs, were reported by Stevens (42) in December, February, and in the late spring and early summer. They have been taken at Departure bay,

from January until April, and the larvae occur in the plankton from February until the end of May. The egg mass is bright yellow when freshly extruded and changes to brown when ready to hatch.

There are three larval stages before the post-larval, corresponding in this respect to some species of the genus as described by Webb (46), but the larvae of this species hatch in a slightly more advanced state of development than do the European forms. This was also found to be the case in some of the Pandalids of British Columbia (5).

First larva about 3.7 mm. in length, measured from tip of rostrum to posterior margin of telson. Transparent, with a blue tinge to body, and liver showing through carapace as an olive green organ. Yellow around eyestalks, and a red chromatophore near tip and another on proximal part of antennule. Red pigment on carapace anterior to gastric mill, as well as on proximal part of first abdominal segment and on median part of telson (two chromatophores). A branching red chromatophore on basal part of non-functional third maxilliped.

Larva (Fig. 5, A, B) of the same type as those described by Webb (46). Carapace with rounded edges posteriorly and small, sharp-pointed rostrum reaching about one-third length of antennules. Abdomen composed of five segments and deltoid telson. Posterior margin of telson indented medially with a spine, a fine hair and five plumose setae on each half. Segments of abdomen smoothly rounded posteriorly, without dorsal or lateral spines.

Tubular antennule (Fig. 6, A) quite long, with several aesthetes on inner margin and terminally, and a long plumose seta a short distance from tip. Antenna (Fig. 6, B) large: protopodite with a single spinous projection ventrally, endopodite tubular with three long plumose setae terminally, and broad exopodite terminating in a stout spine and bearing eight long and one short plumose setae on inner margin.

Mandibles (Fig. 6, C) without incisor processes, and molar surfaces cut into a number of small teeth. Maxillule (Fig. 6, D) with wide clearly defined endites on protopodite, each bearing eight spines, and the two-jointed endopodite with two plumose setae on distal portion of internal edge of first segment and six on second (four terminal and two sub-terminal). Lamellate maxilla (Fig. 6, E) with endites of protopodite bilobed: coxopodite bearing ten and four setae and basipodite five and six. Endopodite with five plumose setae, but is not clearly separated from protopodite like Brachyuran zoea, and scaphognathite narrow, with about 11 plumose hairs on margin.

First maxilliped (Fig. 6, F) provided ventrally with a number of bristles, both plumose and simple: two on coxopodite and about 11 on basipodite. Endopodite five-jointed, and segments usually with three, three, one, two and five bristles respectively on ventral distal part of segments, and fine hairs on the second, third and fifth segments dorsally. Four swimming setae on exopodite. No setae on coxa and basis of second maxilliped (Fig. 6, G) but four swimming setae on exopodite. Endopodite four-jointed, with third segment

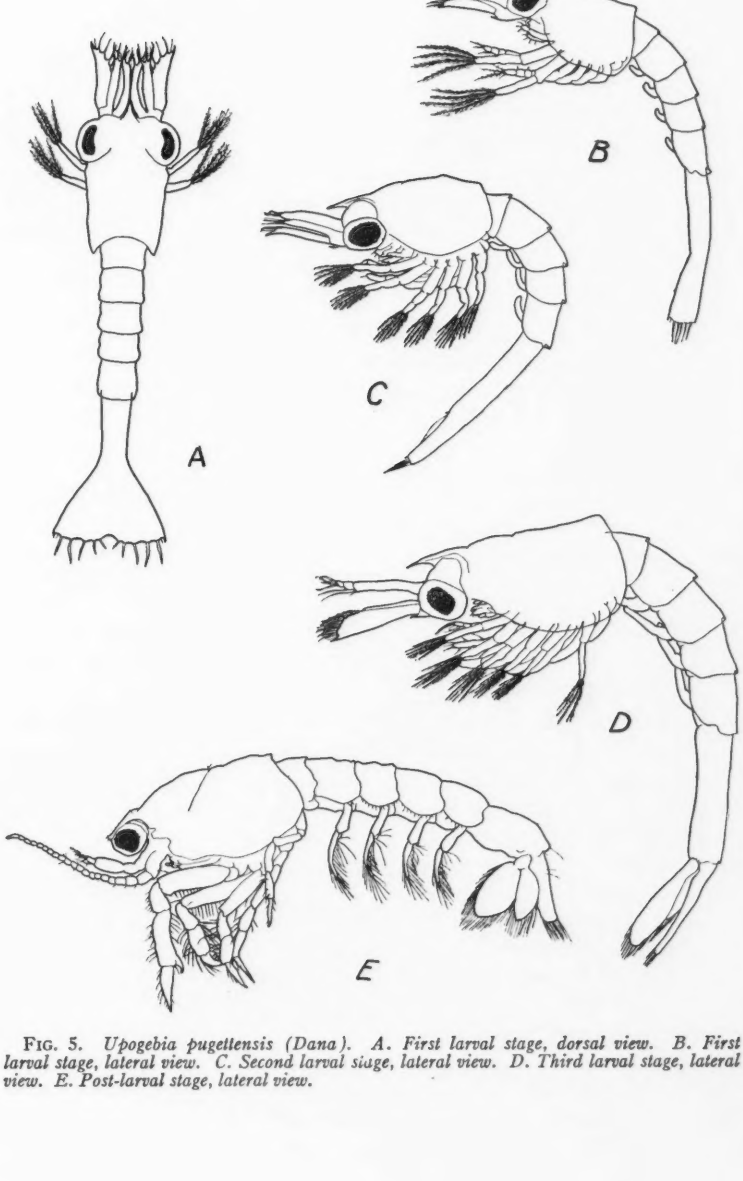


FIG. 5. *Upogebia pugettensis (Dana). A. First larval stage, dorsal view. B. First larval stage, lateral view. C. Second larval stage, lateral view. D. Third larval stage, lateral view. E. Post-larval stage, lateral view.*

equal in length to the other three, and segments bear one, one, two and three setae respectively. Large, non-functional exopodites present on rudimentary third maxilliped and on first three pairs of pereiopods. Endopodites on all these anlagen well developed. Four pairs of pleopods will be developed, indicated in first stage by knobs on abdomen.

Second Stage (Fig. 5, C; Fig. 6, H-L). Second larva (Fig. 5, C) about 4.4 mm. in length and similar in color to first. Sixth abdominal segment not yet separated from telson (Fig. 6, H) which is similar in shape to that of first stage, but has an extra pair of plumose setae medially and a small median tooth on posterior margin. Fourth pair of setae now considerably longer and stouter than others. Uropods show clearly through integument but still fully enclosed within telson membrane.

Antennule (Fig. 6, I) larger and tip cut into two knobs: anlagen of flagella of adult. Outer is larger and bears aesthetes, and more slender inner knob sharp-pointed, and bears fine setae. Several plumose setae on inner and a tuft of fine hairs on outer margin of peduncle. Antenna (Fig. 6, J) more elongate than that of first stage and endopodite still bears three setae. A spine on disto-lateral part of protopodite in addition to toothed one of first stage.

Now six setae on exopodite of both first and second maxillipeds. Third maxilliped (Fig. 6, L) with functional exopodite bearing six setae and a small bare endopodite which arises at proximal part of basipodite and reaches to its tip. Functional exopodites now on first, second and third pereiopods; those of the first two bearing six setae and that of the third, five. These appendages are similar to third maxilliped except that their endopodites larger; decreasing in size posteriorly. Fourth and fifth legs small and non-functional, but showing indications of segmentation. Pleopods quite large but show no subdivisions.

Third Stage (Fig. 5, D; Fig. 6, M-O). Third stage (Fig. 5, D) about 5.4 mm. in length and similar in color to the earlier stages. Abdomen now composed of six segments and telson (Fig. 6, M), which is more spade-shaped and bears three teeth on each side (with a fine hair between the two lateral), and four pairs of plumose setae medially. There is a median tooth.

Antennule (Fig. 6, N) like that of second stage but plumose setae on margin of peduncle have greatly increased in size and number. Now a swelling proximally. Antenna (Fig. 6, O) large, with endopodite equal in length to exopodite and no longer bearing terminal setae. Segmentation of flagellum of post-larva can be seen through the thin integument of endopodite for some time before ecdysis.

Palp on mandible is now quite large but rest of appendage not appreciably increased in size. Maxillule similar to that of second stage. Scaphognathite of maxilla still narrow.

Six setae on exopodite of first maxilliped and of third pereiopod and seven on rest. No indication of thumb on first pereiopod. Long and slender

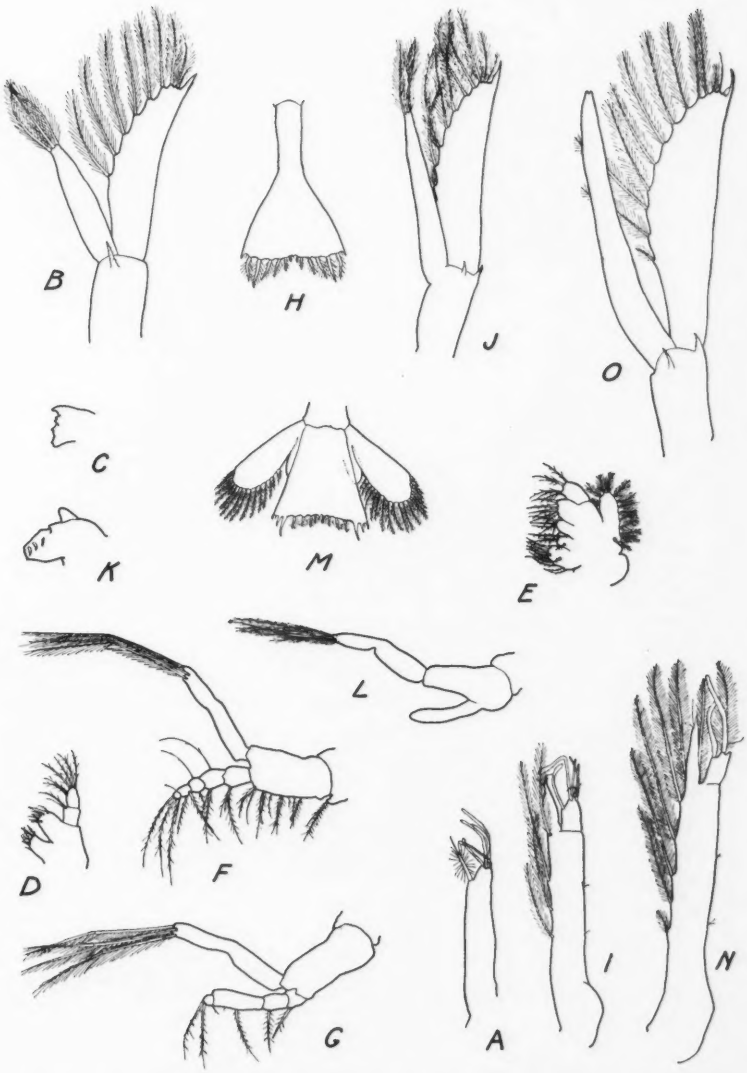


FIG. 6. *Upogebia pugettensis (Dana). First larval stage. A. Antennule. B. Antenna. C. Mandible. D. Maxillule. E. Maxilla. F. First maxilliped. G. Second maxilliped. Second larval stage. H. Telson. I. Antennule. J. Antenna. K. Mandible. L. Third maxilliped. Third larval stage. M. Telson. N. Antennule. O. Antenna.*

anlagen of pleopods show but slight indication of divisions. Uropods separate from telson: exopodite large with about 15 long plumose setae on medial margin but endopodite small and naked.

Post-larval Stage (Fig. 5, E). Post-larva about 4 mm. in length. Very transparent with a few red pigment spots, situated on anterior part of carapace, on first, second, third and sixth abdominal segments, on tips of antennules and on propodi of all the pereiopods. Post-larva (Fig. 5, E) of adult form. Obtuse rostrum with a number of bristles and small knobs distally, and lateral teeth practically obsolete. Abdomen clearly segmented but pleura narrow. Telson rectangular with long plumose setae on distal margin.

Appendages differ from those of adult mainly in clarity of segmentation and in numbers of setae. Flagella of antennule short, inner one of a single segment and outer of about three. Scale of antenna small and square. Mouth parts show no striking differences from those of adult.

A small tooth or thumb on medial distal corner of propodus of first and fifth pairs of pereiopods. Pleopods present on second to fifth segments of abdomen and of much the same proportions as adult appendages. Setae are, however, fewer in number and comparatively longer. Uropods proportionately longer and more rounded than those of adult.

Genus *Paguristes*

Issel (22) described the larval stages of *Paguristes oculatus* Fabr. from Naples. He gives but two zoeal stages and one glaucothoe, which is a more abbreviated larval history than that of any other hermit crab yet described. It seems possible that he might have missed the normal first stage, as his description of what he considered to be the first stage has the usual second stage characteristics, with the exception of the four setae on the exopodites of the first and second maxillipeds and the non-functional third maxilliped (which, however, in his figure shows short terminal setae).

P. turgidus (Stimpson) has a short larval phase in the laboratory, reaching the post-larval in about one-sixth the average time required for other Anomura. The larvae are large when hatched and increase very little, if at all, in size during development: the post-larva is smaller than the first zoea. The integument is thin and the cast-off skins are easily missed in the culture jars.

As the time spent in each stage is so short, it seems quite probable that Issel might have missed a stage, or confused two. Dr. A. B. Needler pointed out to the writer that all first stage decapod larvae have sessile eyes, which become stalked in the second stage. Issel states quite definitely that they are stalked in his first stage larva (page 348) "i suoi occhi, relativamente piccoli, sono portati da brevissimi peduncoli." His figures do not agree in several instances with his description, *i.e.*, he puts segments in such structures as the third maxilliped so as to make an abnormal (as far as other Anomuran larvae are concerned) appendage. In several appendages he fails to separate

the dactylus from the propodus, etc. The unarmed mouth appendages are unusual but might be found in such a species that apparently does not feed in the larval phase. He figures the abdomen of the first stage as composed of seven segments and the telson, which is ridiculous, and especially so as the second stage shows five segments.

The antennule in Issel's figure of the first zoea shows the same degree of development as is found in the second zoea of *P. turgidus* and other Anomura. Also the mandible bears a palp, which is not present in the first stage of *P. turgidus* but develops in the second. The scaphognathite of the maxilla of *P. oculatus* is divided into parts in the same way as that of *P. turgidus*. The pleopods and uropods of the former are in the same state of development as those of the second stage of *P. turgidus*. The metazoea and glaucothoe of both species differ mainly in such characters as might be specific or due to inaccurate observation.

Menon (28) describes a series of larvae from Madras plankton belonging apparently to the subfamily Upogebiinae. These larvae show some interesting intergradations between *Upogebia* and *Paguristes*. The Madras form differs from both of these in having a more prolonged larval life history (five stages, instead of three or four), in the presence of epipodites on thoracic appendages 2-6, and *appendices interna* on the pleopods of the post-larval stage.

The Madras larvae resemble *Paguristes* and differ from *Upogebia* in the presence of lateral spines on the posterior margin of the fifth abdominal segment, and in the absence of a median spine on the telson until the metazoea. These two characters are the main differences between *Paguristes* and *Upogebia* in the early stages.

Paguristes turgidus (*Stimpson*) (Figs. 7, 8 and 9)

Females with freshly laid eggs (which hatched in late August and early September) were found in July near Nanaimo. To judge from the state of the eggs on specimens obtained from the west coast of Vancouver island, the spawning season there is the same as that of the east coast. The egg mass was coral red, changing to yellow as development proceeded.

There are three larval stages and probably only one post-larval. The glaucothoe did not survive long enough to moult again. The glaucothoe was obtained in the laboratory five and a half days after hatching in one instance and eight in another. *Pagurus* usually requires at least 30 days to reach the same state of development, but apparently *Paguristes* takes very little food during development and increases little in size, while *Pagurus* nearly doubles.

First stage about 4.5 mm. in length. Very transparent, with russet-red and yellow chromatophores. Chitin of antenna faintly tinged with blue, and liver yellow. Red pigment in a band anterior to liver; on carapace posterior to eyestalks, medio-laterally and marginally above maxillipeds; on abdomen laterally in paired chromatophores at junction of fourth and fifth segments and ventro-medially at bases of lateral spines of fifth segment: on

telson medially and across proximal part: on eyestalks, on bases of antennae, ventrally beneath eyestalks, at attachment of maxillae, on each mandible, on distal part of bases of first and second maxillipeds and on median part of endopodite and exopodite, and on third maxilliped. Yellow pigment medio-posteriorly on carapace; at bases of spines on second and third abdominal segments and margin of spatulate part of telson.

First stage (Fig. 7 A, B) stout. Rostrum narrow and less than one-third length of carapace, which is smoothly rounded posteriorly, resembling in this feature Thalassinid larvae rather than Pagurid. A sharp "branchiostegal" spine. Abdomen stout and dorsum of second segment produced posteriorly into a large median spine. Same regions of third, fourth and fifth segments similarly produced, but as smaller spines. Fifth segment has in addition a pair of spines on the postero-lateral margins. Telson roughly triangular and margined with seven setae on each side; the seventh (lateral) pair simple, the sixth very small and plumose, and the remainder large and plumose: fourth the longest.

Antennule (Fig. 8, A) slightly longer than rostrum, slender with one plumose seta near tip and about six aesthetes apically. Antenna (Fig. 8, B) with stout basis, narrow spinous process ventrally, and broad, flat endopodite, ending in a curved spine and bearing 12 long plumose setae on medial margin. Exopodite cylindrical, with three long plumose setae terminally.

Mandibles (Fig. 8, C) have cutting surface composed of a number of fine teeth. A slight knob on dorsal surface indicative of future palp. Maxillule (Fig, 8, D) with six plumose setae on coxopodite, two spines and two setae on basipodite and a three-jointed endopodite with one seta on distal margin of second segment and three on third. Maxilla (Fig. 8, E) with about ten setae on bilobed coxopodite, nine on basipodite, six on endopodite and ten soft plumose hairs on scaphognathite. An indication of the division of the latter into what is apparently a large exopodite and a small epipodite, covered over by a thin membrane.

First maxilliped (Fig. 8, F) composed of broad basis bearing ten bristles, exopodite with four swimming setae, and endopodite of five segments bearing respectively three, three, one, two and five setae ventrally and long fine hairs on dorsal side of second and third segments. Second maxilliped (Fig. 8, G) with three bristles on basis, four on exopodite and two, two, two and five respectively on segments of endopodite, with fine hairs on dorsal part of second segment. Third maxilliped devoid of setae and non-functional in this stage, but its exopodite reaches to end of basis of second maxilliped and endopodite about half length of exopodite.

Remaining thoracic appendages non-functional but large and well developed and hidden by margins of carapace. First and fifth pereiopods show traces of chelate tips and position of future joints can be seen in all. Fifth pereiopods medially placed and hidden under incurved anterior limbs, which are tucked up under thorax. Anlagen of pleopods not yet apparent.

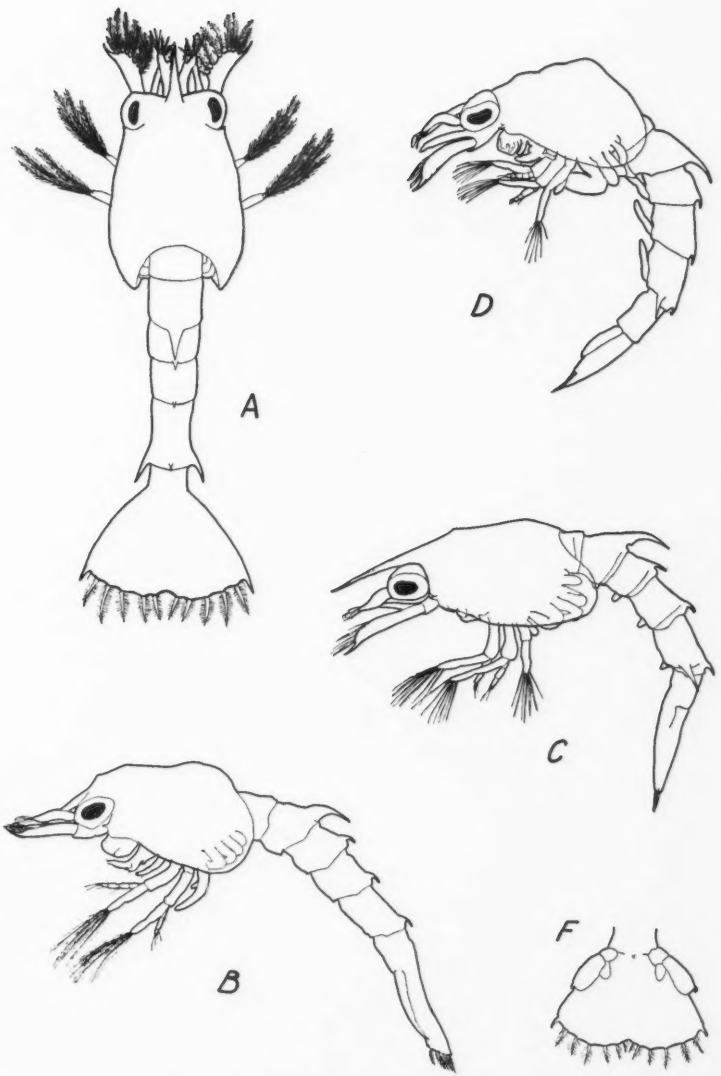


FIG. 7. *Paguristes turgidus (Stimpson). A. First larval stage, dorsal view. B. First larval stage, lateral view. C. Second larval stage, lateral view. D. Third larval stage, lateral view. F. Third larval stage, telson and uropods, ventral view.*

Second Stage (Fig. 7, C; Fig. 8, H-K). Second stage of *Paguristes turgidus* (Fig. 7, C) has not increased in size and its coloration is similar to first stage. Main differences are that eyes now rather elongated and stalked and that sixth segment of abdomen is separated from telson. Telson of same shape but has an extra pair of setae on medial part of posterior margin and the formation of the uropods can be seen through the thin integument. The rudimentary appendages increase in size during this stage so that it would at first glance appear that several stages were present, but there is only one more moult before the post-larval stage.

Antennule (Fig. 8, H) has increased in complexity. Plumose seta now situated on a protuberance, below which are two large plumose bristles, and aesthetes arranged in rows toward tip, which is separate from rest of appendage. Antenna not perceptibly changed.

The unusually well developed mandible (Fig. 8, I) has a naked, knob-like palp. In most pagurid species this does not appear until the last larval or post-larval stage. Maxillule similar except that the two small setae on basipodite have increased in size and are almost as large as the spines, and two additional small setae present now. Maxilla (Fig. 8, J) similar to that of first stage, except that epipoditic part is greatly increased in size and quite bare of setae and separate from exopoditic portion.

Seven setae on the exopodite of first maxilliped; about same number of setae on segments of endopodite but fine hairs of first stage replaced by long fine setae. Second maxilliped has now eight swimming setae on exopodite, and a fine seta on dorsal part of third segment of endopodite. Third maxilliped (Fig. 8, K) has exopodite functional and bearing seven setae. Endopodite quite large, comes off basis more proximally than does exopodite but not yet functional, although showing indications of segmentation.

Pereiopods large and show joints through the thin chitin. Pleopods present as distinct knobs.

Third Stage (Fig. 7, E). Third stage of *Paguristes turgidus* slightly smaller than second and similarly colored. Telson (Fig. 7, E) is of same shape but now two additional pairs of setae on margin medially and uropods separate.

Antennule like that of second stage but segments of appendage of following stage clearly discernible through thin integument. Endopodite of antenna now subequal in length to exopodite and a small spine distally on ventrolateral margin of protopodite.

Palp on mandible considerably larger than that of second stage. Two more small setae on basipodite of maxillule. Epipoditic part of scaphognathite longer and finger-like and bears no setae on margin but exopoditic provided with 16 soft plumose hairs.

Maxillipeds little changed except that first has now eight swimming setae on exopodite. Pereiopods well developed and segmentation of next stage clearly visible. Pleopods large: small endopodite and large exopodite. Uropods with large exopodite, terminating in a curved hook-like spine and with small endopodite.

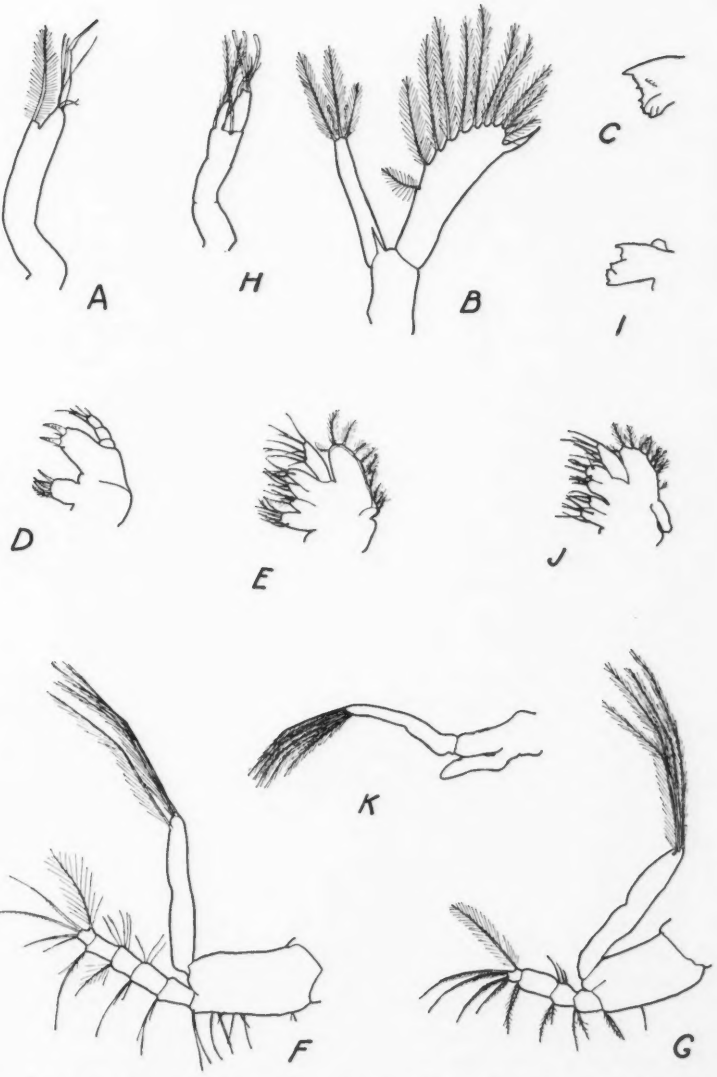


FIG. 8. *Pagurisles turgidus (Stimpson). First larval stage. A. Antennule. B. Antenna. C. Mandible. D. Maxillule. E. Maxilla. F. First maxilliped. G. Second maxilliped. Second larval stage. H. Antennule. I. Mandible. J. Maxilla. K. Third maxilliped.*

Glaucothoe (Fig. 9). Glaucothoe (Fig. 9, A) about 3 mm. in total length, with carapace about 1 mm. Of the usual glaucothoe form, but with subequal chelae and only slightly asymmetrical uropods. Like the zoea, very transparent, with yellow tinged legs and russet-red chromotophores scattered over body. Red chromatophores on rostrum; on ventro-lateral edge and median dorso-posterior margin of carapace: a pair on fifth abdominal segment, numerous around margin of telson; on medial dorsal part of eyestalks, on bases of antennae, on distal part of propodi of chelae, on second and third pairs of walking legs, and on each part of uropods. Carapace with blunt rostrum. Segments of abdomen of equal length, but anterior wider than posterior. Telson hexagonal, with two lateral spines and ten long bristles distally.

Antennule (Fig. 9, B) large, with specialized setae and short bristles on first segment of peduncle; inner flagellum two-jointed and small five-jointed outer, armed with scattered bristles and aesthetes. Antenna (Fig. 9, C) has large tooth on peduncle, scimitar-shaped scale and eight-jointed flagellum, with bristles increasing in length and number toward tip.

Mandibles (Fig. 9, D) with well developed palp bearing a few short bristles on distal margin of third segment. Cutting edge rounded in right mandible and somewhat triangular in left. Maxillule (Fig. 9, E) has broad endites with short spines and bristles and endopodite of two segments, of which proximal is large and bears two bristles, and distal very small. Maxilla (Fig. 9, F) has shallow bifid endites with few bristles, finger-like endopodite, and rather narrow scaphognathite, which is divided into exopoditic and epipoditic portions by a slight fold.

First maxilliped (Fig. 9, G) with poorly developed exopodite and endopodite, almost devoid of setae, and narrow endites of protopodite with poorly developed bristles. Second maxilliped (Fig. 9, H) has large exopodite with five plumose setae on terminal segment, and five-jointed endopodite with a few small bristles distally. Third maxilliped (Fig. 9, I) also has large exopodite, with six plumose setae, and five-jointed endopodite with bristles on lateral margin and tip.

First pereiopods are chelate and subequal, with scattered spines and bristles on all segments. Second and third pereiopods long and slender. Fourth pereiopod smaller than second or third, with suctorial setae on propodus, and dactylus short, terminating in a stout claw. Fifth pereiopod also small but chelate: propodus flattened distally and flattened dactylus fits into groove of propodus; suctorial setae and long bristles on tip of appendage. Pleopods all equipped with elongate protopodites, small endopodites each with two ciccinnuli, and exopodites each bearing nine plumose setae. Uropods slightly asymmetrical and each composed of a short protopodite, with a single bristle, a stout exopodite margined with long bristles and suctorial setae, and a short endopodite similarly supplied.

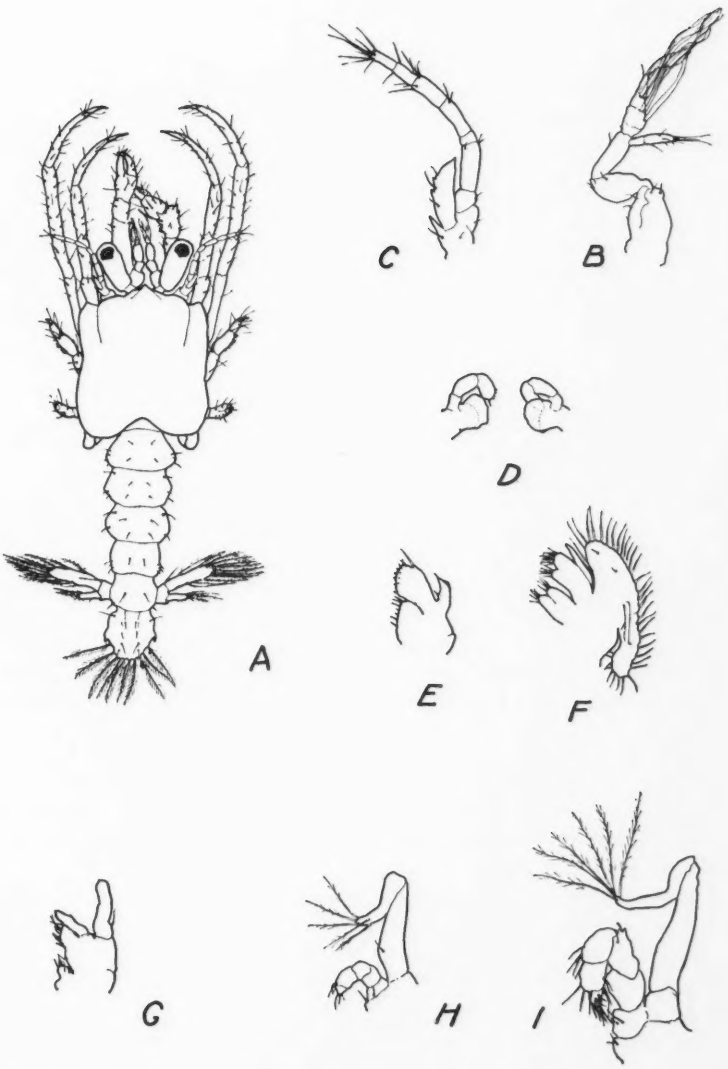


FIG. 9. *Paguristes turgidus (Stimpson). Glaucothoe. A. Dorsal view. B. Antennule. C. Antenna. D. Mandibles. E. Maxillule. F. Maxilla. G. First maxilliped. H. Second maxilliped. I. Third maxilliped.*

GENUS *Pagurus*

Rathke (36, 37) described the larval and post-larval stages of *Pagurus bernhardus*. The only important studies on *Pagurus (Eupagurus)* are by Sars (39) for the European forms and Thompson (45) for New England species. The larvae of *Pagurus beringanus* described below are very like those of *P. bernhardus* as described by Sars, and differ from those of *P. longicarpus* and *P. annulipes* by Thompson mainly in the absence of setae on the endopodite of the antenna in the first two stages.

Pagurus beringanus (Benedict) (Figs. 10 and 11)

Berried females of *Pagurus beringanus* (Benedict) were obtained in March, near Vancouver, and from May until August at different points off Vancouver island. The egg mass changed from brownish black to a grayish brown during the incubation period. The eggs hatched the last day in July and the first young crab was obtained in the laboratory 40 days later, after passing through four zoeal stages and one glaucothoe.

First stage (Fig. 10 A, B) about 2.4 mm. in length. Yellowish in color; rostrum, antennae, mouth parts and maxilliped exopodites blue tinged. Liver pale yellow. Red pigmentation on median anterior part of eyestalks, dorsomedially behind eyes, on carapace above bases of maxillipeds, internally around and beneath anterior part of liver, on bases of mouth parts, on bases of maxillipeds, on dorsal part of third abdominal segment, at junction of fifth segment and telson, and on anterior part of telson.

Body slender and elongate. Carapace has a long sharp-pointed rostrum about equal in length to rest of carapace and over-reaching antennae. Carapace produced posteriorly into a pair of downward curving sharp teeth. Abdomen fairly stout, of five segments, with posterior dorsal margin of second to fifth cut into four teeth, and fifth with long lateral spines in addition. Telson rather wide, triangular-shaped, and bearing seven pairs of spines and setae on posterior, medially indented margin. Lateral pair (seventh) short spines, next (sixth) minute hairs, and remainder, sharp-pointed finely serrate setae, of which the fourth is longest and rest decrease in length, five, three, two, and one respectively.

Antennule (Fig. 10, C) cylindrical, with a long plumose seta subterminally and two aesthetes at tip. Antenna (Fig. 10, D) has a short spinous process on protopodite, a narrow smooth endopodite about three-fourths length of wide exopodite, which has five plumose setae on middle third of medial margin.

Mandibles (Fig. 10, E) of usual type, with fine teeth on cutting edge. Maxillule (Fig. 10, F) has five long and two short barbed bristles on coxopodite, two toothed spines and two setae on basipodite, and no, one and three bristles on segments of endopodite. Maxilla (Fig. 10, G) lamellate, with about nine setae on both bilobed coxopodite and basipodite, seven on endopodite and five soft plumose hairs on narrow scaphognathite.

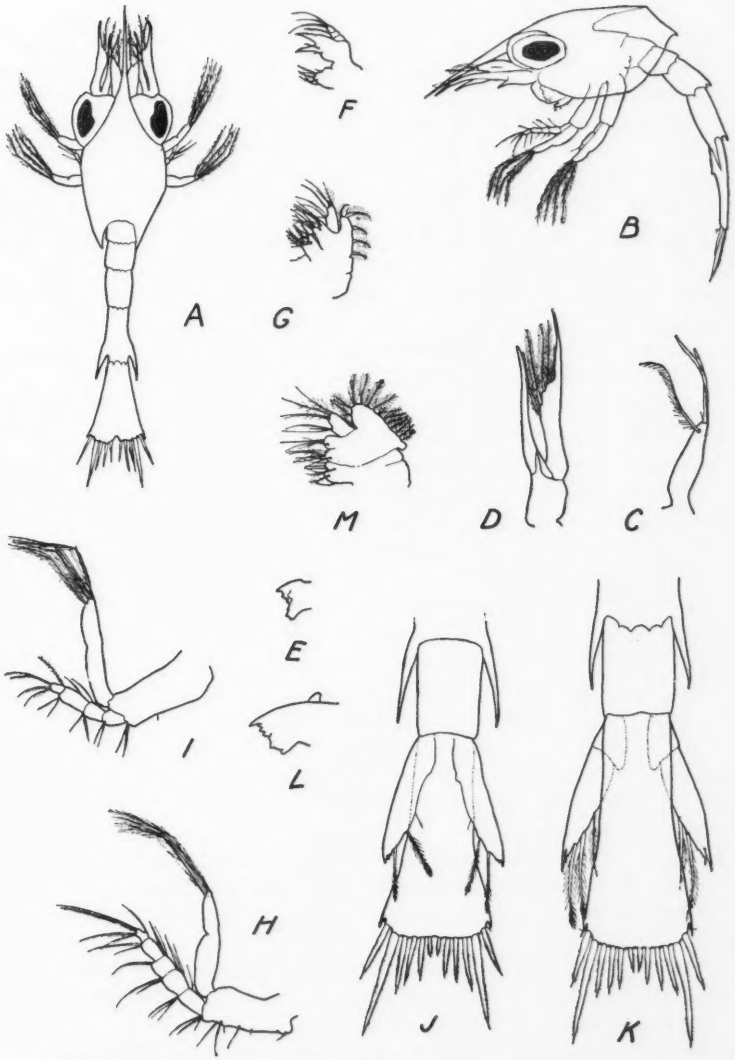


FIG. 10. *Pagurus beringanus (Benedict). First larval stage. A. Dorsal view. B. Lateral view. C. Antennule. D. Antenna. E. Mandible. F. Maxillule. G. Maxilla. H. First maxilliped. I. Second maxilliped. Third larval stage. J. Telson and uropods. Fourth larval stage. K. Telson and uropods. L. Mandible. M. Maxilla.*

First maxilliped (Fig. 10, H) has about nine bristles on basis, four swimming setae on exopodite and three, two, one and five respectively on ventral side of segments of endopodite and soft filaments on dorsal side of first, second and third. Second maxilliped (Fig. 10, I) has three bristles (one serrate) on basis, four on exopodite, and two, two, two and five on segments of endopodite ventrally and filaments dorsally on second and third segments. Third maxilliped non-functional: uniramous and tucked forward under thorax, between bases of other two.

Limb buds small and no signs of pleopods.

Second stage about 2.9 mm. in length and similar in color to first stage. Slight indication of separation of sixth segment of abdomen from telson, but not yet a definite somite. Telson has now an additional pair of small setae medially on posterior margin. Eyes stalked.

Antennule with plumose hair elevated on a small peduncle. Endopodite of antenna now nearly equal in length to exopodite.

Mandibles unchanged in shape. Maxillule has two more spines on basipodite. More setae (eight) on scaphognathite of maxilla than in first stage.

First maxilliped has seven plumose setae on exopodite and filaments replaced by soft plumose hairs on first, second and third segments of endopodite. Second maxilliped also has seven setae on tip of exopodite and a soft hair dorsally on second segment of endopodite. Third maxilliped has six setae on exopodite and no endopodite.

Rudimentary pereiopods slightly larger than those of first stage and appear in lateral view as four knobs covered by carapace. Pleopods not yet visible. Anlagen of uropods can be seen through thin integument of telson.

Third stage (Fig. 10, J) about 3.2 mm. in length. Now six segments in abdomen. Teeth on posterior margins of second and third segments obtuse and lateral spines of fifth segment equal in length to sixth segment. Telson (Fig. 10, J) similar except that uropods now free and fourth pair of setae almost twice as long as any of the others.

Knob on antennule increased in size and aesthetes increased in number. Antenna reaches nearly to tip of rostrum and endopodite longer and wider than exopodite. Small spine on protopodite near base of exopodite.

Mandibles and both pairs of maxillae show no appreciable change except in size.

First maxilliped has seven swimming setae on exopodite and second eight. Third maxilliped has seven and endopodite arises near base of protopodite and is small, with one terminal seta.

Pereiopods still small but tip of first one notched, indicative of chela. Fifth pair hidden under thorax and cannot be seen in a lateral view. Thickenings under integument where pleopods will appear in later stages. Uropods (Fig. 10, J) large, with tip cut into three small teeth, and three stout setae on medial margin; endopodite only a slight protuberance on medial proximal margin.

Fourth stage (Fig. 10, K-M) about 3.6 mm. in length. Differs little from third stage except in size and development of non-functioning appendages, which reach their maximum size in this stage. Sixth segment of abdomen and telson (Fig. 10, K) have elongated considerably.

Two flagella of antennule clearly defined; inner one, bare knob, with a long plumose seta at base and outer with three rows of aesthetes. Antenna similar to that of third stage.

Left mandible (Fig. 10, L) has a sharp dorsal tooth and a wide ventral one on molar process, but right composed of a number of fine teeth. Both equipped with a small bare palp. Maxilla (Fig. 10, M) has about a dozen plumose setae on scaphognathite.

Both first and second maxillipeds have eight swimming setae on exopodites. Third maxilliped has seven, and two setae on endopodite.

Chelate nature of first pereiopod now quite apparent. Pleopods long and slender, but endopoditic part not clearly defined. Exopodite of uropods (Fig. 10, L) now separate from remainder of appendage. Endopodite still just a projection of medial distal corner of protopodite.

Glaucothoe and Adolescent Crab (Fig. 11, A, B). Glaucothoe of *Pagurus beringanus* about 1.9 mm. from tip of rostrum to end of telson. Quite transparent, with yellowish tinge and scarlet and black chromatophores: black on either side of liver, and on bases of third maxillipeds, and red irregularly placed on posterior part of carapace, on second, third and sixth abdominal segments, and on propodi of chelipeds.

Glaucothoe (Fig. 11, A) small but fairly stout, with an obtuse rostrum and unarmed carapace. First segment of abdomen narrow, second wide, and rest taper to rather narrow sixth segment. Telson elongate, and subrectangular with eight terminal setae. Eyestalks large and cylindrical and their scales small and sickle-shaped.

Antennule has an elongate peduncle and inner flagellum longer than outer, which has aesthetes only on proximal half. Appendage sparsely armed with bristles. Antenna with triangular scale and flagellum of about 10 segments.

Mandibles poorly developed and small, with narrow molar portion and fair sized palp. Endites of protopodite of maxillule large, but with few and weak bristles and endopodite small and feeble. Endites of maxilla slightly bilobed and fringed with setae; endopodite small and closely applied to basipodite and scaphognathite narrow.

First maxilliped poorly developed: endites rounded and armed with a few weak bristles on margin, endopodite small and undifferentiated, and two-jointed exopodite tipped with fine hairs. Second maxilliped has a five-jointed endopodite, poorly provided with bristles and a large two-segmented exopodite ending in a brush of fine setae. Third maxilliped well developed, with a large endopodite, well provided with bristles distally and a short exopodite terminating in setae. On the whole the mouth parts are poorly developed and indicate a microplankton diet at this time.

First pereiopod chelate and toothed on cutting margins. Right larger than left. Second and third pereiopods long, slender and simple. Fourth short, somewhat subchelate, and propodus provided with a few suctorial setae. Fifth also small with short dactylus and propodus tipped with three long bristles and several suctorial setae.

Pleopods of three parts with wide protopodite, small endopodite bearing two ciccinnuli and exopodite with eight, nine, eight and six plumose setae respectively. Left uropod slightly larger than right and both composed of short protopodite, wide scimitar-shaped exopodite margined with plumose and suctorial setae and small endopodite bearing one or two setae.

Adolescent crab (Fig. 11, B) like adult except for the usual juvenile characteristics.

Orthopagurus schmitti (*Stevens*) (Fig. 11, C, D)

An ovigerous female of *Orthopagurus schmitti* (Stevens) has not yet been obtained, but on April 27, 1933, plankton was taken off Horswell point, containing metazoeae and glaucothoe of a hermit crab. These were kept in rearing jars until the adolescent stages appeared. These clearly showed the characters and coloration of *Orthopagurus*, so that it is with a fair degree of certainty of identification that these stages are compared to those of hermit crabs and sand shrimps reared from the egg.

Last zoeal stage about 7 mm. in length. Blue tinged antennae, mouth parts and pereiopods, except chelae which are yellow. A mass of scarlet pigment around liver.

Last larval stage (Fig. 11, C) of *Orthopagurus* differs from that of *Pagurus beringanus* mainly in size, color and presence of more setae on certain appendages of former. Carapace produced anteriorly into a long sharp-pointed rostrum and posteriorly into rather obtuse downward-pointing teeth. Dorso-posterior margins of third to fifth abdominal segments cut into four sharp teeth, and lateral spines of fifth segment are about half length of sixth segment. Telson (Fig. 11, D) elongate, like that of *Pagurus*, except that fourth pair of spines are only slightly longer than others.

Antennule like that of *Pagurus* except that there are two long plumose setae at base of inner flagellum, instead of one. Endopodite of antenna reaches to tip of rostrum, and is longer than exopodite, which has nine plumose setae on medial margin.

Mandibles, maxillules and maxillae very similar to those of *Pagurus* except in size.

Maxillipeds like those of *Pagurus* except that they all have eight swimming setae on their exopodites, and that there are three setae on endopodites of third maxilliped. Pereiopods and pleopods of usual degree of development for this stage. Large uropods (Fig. 11, D) nearly as long as telson, and tip of exopodite cut into several elongate teeth, while medial margin bears six plumose setae. Endopodite a small unarmed projection of protopodite.

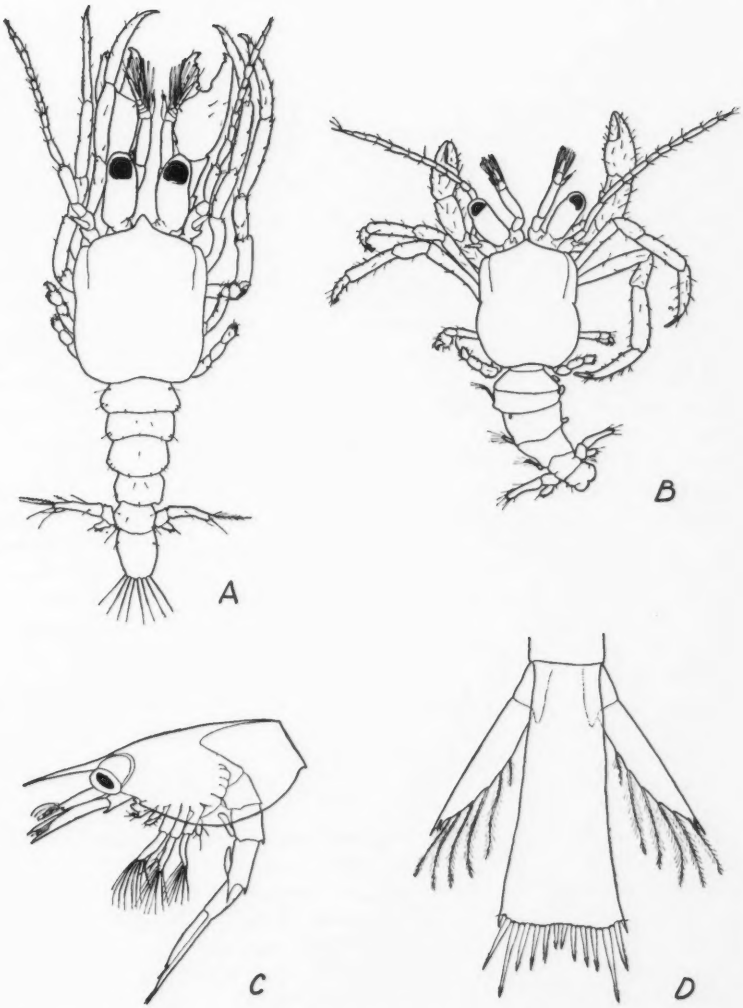


FIG. 11. *Pagurus beringanus (Benedict). A. Glaucothoe, dorsal view. B. First adolescent crab, dorsal view. Orthopagurus schmitti (Stevens). Last larval stage. C. Lateral view. D. Telson and uropods.*

Glaucothoe and Adolescent Crab. Glaucothoe resembles that of *Pagurus beringanus* except that it is nearly twice its size (about 3.5 mm. in length). A pale brown color, with fine red chromatophores on eyestalks and legs, and a large scarlet patch around gastric and heart regions.

The glaucothoe of the two species, in addition to size and coloration, also differ in the form of their chelae and tail-fans. Chelae of post-larva of *Orthopagurus schmitti* are proportionately narrower and fingers longer than those of *Pagurus beringanus*, and inner margins of carpus and propodus are toothed. Uropods longer and narrower and more heavily armed with setae. Telson elongate, with eight long setae on curved distal margin and several short bristles on each of lateral edges.

The adolescent crabs may be distinguished by their subequal uropods and coloration.

Discussion and Conclusions

The present system of classification of Anomura is based entirely on adult characters. As was pointed out by Gurney (16) ontogenetic stages should be of great value in classification and should not be neglected. The adult phase is but one stage in the cycle and therefore should not be given the importance denied another. There naturally are adaptive modifications in the larvae that present difficulties, but such convergences are equally present in the adults, so that this does not necessarily detract from the value of the larvae in a study of relationship. *Upogebia* has but a vestigial antennal scale in the adult phase, while in the larvae, the scale (exopodite), is large and well developed. It is of course essential to realize that the useful characters of the larvae are usually not those structural features used in distinguishing the adults. The conclusions drawn from the small proportion of the larvae that have been studied suggest that the larvae may be grouped by such small differences as the reduction in size of the one pair of setae on the margin of the telson or the absence of setae on the endopodite of the antennae, and these characters would appear to be at least as reliable as many of the adult features that are now considered important in the taxonomy. Unfortunately knowledge of adult morphology is in the majority of cases superficial, and is concerned mainly with the parts that exhibit obvious differences which are of value for ease of separation and of identification. The life histories and larval stages of only a small proportion of the total number of species have been investigated, but larval stages of nearly every family of Decapoda are now known, through the extensive work of Lebour and Gurney particularly. Unfortunately for the problem at hand, the Anomura have received considerably less attention than the other tribes. Hence, morphological information about all stages being scanty and specialization being well marked in the group, generalizations are as yet unsafe; evidence now available permits only tentative suggestions concerning the possible interrelationships.

In the present system of classification the genera *Paguristes* and *Pagurus* are placed in two subfamilies of the family Paguridae. Superficially these are alike, but on morphological grounds, based on both the adult and larval

phases, it would appear that their resemblances are the result of convergence due to their specialized mode of life. On the other hand, *Pagurus* and *Orthopagurus* are members of the same subfamily, and this position is confirmed by a study of their anatomy, despite the fact that on the surface they seem more unlike than *Pagurus* and *Paguristes*. *Upogebia*, placed in a different superfamily exhibits a number of characters that are considered primitive. *Paguristes*, in such features as are unmodified by the environment, shows the same primitiveness, which, however, is lacking in the other two under consideration.

In an attempt to determine genetic relationships no hint may be obtained from the study of fossil remains. Fossil Anomura are rare, only the genus *Callianassa* having been found as yet and as early as the Mesozoic era. A few specimens of recent genera, such as *Upogebia*, *Paguristes* and *Pagurus* have been described by Rathbun (35) from Tertiary and Quartenary strata, but obviously these are of no value in this connection. Ortmann (33) believes that the Pagurid group could not have originated before the late Cretaceous or early Eocene Periods. Thus relationships can only be surmised by a study of the living forms, where the problem of distinguishing between environmental and ancestral characters is a difficult one. Thompson (45, p. 197), in discussing the Paguridae, says "In fact, the relationships existing between the various genera as a whole, are very obscure. The group is in all likelihood convergent and not natural, although there is reason to believe that most of the genera are genetically related. If convergent, parts of the group may be of different ages, the characteristic mode of life being assumed at different times by various forms."

One would not expect the mouth parts to be greatly modified by the animal's mode of life, especially where feeding habits are alike, and thus any differences to be seen here should be significant in clarifying our knowledge of their affinities. The maxillules, maxillae and first maxillipeds show such features, *Paguristes* and *Upogebia* having apparently primitive characters which are lacking in *Pagurus* and *Orthopagurus*.

Borradaile (9) gives the characteristics which he considered were possessed by the forebears of the present reptant decapods. Among a number of other features which he believed primitive are a stout, curved, three-jointed palp on the mandible; the basipodite of the maxillule broader than the coxopodite and the endopodite of two segments, the second directed outwards; an epipodite on the first maxilliped; the fourth pair of legs not chelate; and many gills. *Paguristes turgidus* has retained these primitive characters which are lost in both *Pagurus beringanus* and *Orthopagurus schmitti*.

As yet few authors have used the larvae in the classification of decapods. Bouvier (11) considered the larvae in his major divisions. Gurney (16) appreciated their importance and made a number of suggestions for the revision of the systematics, based on larval characters. Lebour (23), from a study of the larval stages of the British Brachyura, pointed out affinities previously

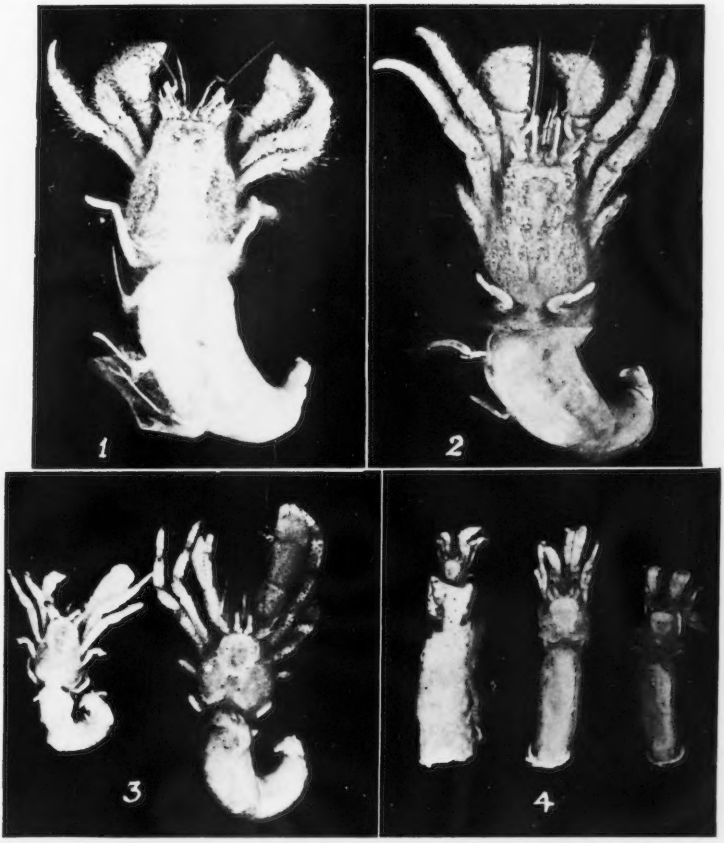
unsuspected when the adults alone were considered. She also has made use of her knowledge of the ontogeny of various decapods in the discovery of new species. She found a previously undescribed species of *Caridion* after studying the larvae in the plankton, and in her paper (24) she quotes K. Stephensen—"but it has astonished me that the two larvae are so well distinguished from one another, for the two adult species are so closely allied that I should hardly have dared to consider them different species if their larvae were unknown." (p. 183). Recently (25) she has found another species of shrimp of the genus *Spirontocaris*, and this was also due to the discovery of a different larva in the plankton. Subsequent investigation showed two distinct types of adults among the collections previously considered to be all *S. cranchii*.

It seems probable that the relationships within the group of Anomura should be more clearly discernible among the larvae (which are all free-living components of the plankton and thus comparable) than among the adults, many of which have become highly specialized in correlation with their varied types of environment.

A study of the larvae of the Anomura with which we are concerned here, suggests the same affinities as have been proposed above in the case of the adults. The larvae of *Paguristes* resemble more those of *Upogebia* than *Pagurus*, and the larvae of *Pagurus* and *Orthopagurus* are closely allied. *Paguristes* and *Upogebia* are alike in the number of larval stages, the size on hatching, the thin integument, the stout build, the absence of teeth on the carapace, the short rostrum, and the three plumose setae on the endopodite of the antenna. *Paguristes* larvae resemble those of *Pagurus beringanus* only in the presence of lateral spines on the fifth segment of the abdomen and in the presence of only two barbed spines on the basipodite of the maxillule in the first stage. The last larval stages of *Pagurus* and *Orthopagurus* differ only in size and in number of setae on some of the appendages. One would not expect to find any trace in the larval or post-larval stages indicating that symmetry has been reacquired in the abdomen of *Orthopagurus*. It has been pointed out by Garstang (15) and by Gurney (16), that any recapitulation of such a modification of the ancestral form would be abnormal, as the larvae of the most asymmetrical forms have as typical an abdomen as do those which are bilaterally symmetrical in all stages of their life cycle.

Before a satisfactory system of classification can be obtained, much more study should be directed to the Anomura. Therefore suggestions for rearrangement, with what evidence is at present available, are quite preliminary, and no real changes can be legitimately made until the life histories of a larger proportion of the members of the tribe are known. However, concerning the genera investigated here, it would seem that the evidence justifies the contention that *Upogebia* and *Paguristes* should not be separated by so great a division as is indicated by their position in separate superfamilies while *Pagurus* and *Paguristes* are included in the same family and separated only into different subfamilies. The facts confirm the position of *Orthopagurus*

PLATE I



1. *Paguristes turgidus (Stimpson), female.* 2. *Paguristes turgidus (Stimpson), male.* 3. *Pagurus beringanus (Benedict), female and male.* 4. *Orthopagurus schmitti (Stevens), in worm tube, male and female.*

and *Pagurus* within the same subfamily. It is hoped that further study of the life histories of decapod Crustacea will result in a better understanding of the genealogy of the components of the group and in a more natural classification.

Acknowledgments

Facilities for the collection of the adult Anomura and the rearing of their larvae were provided by the Biological Board of Canada, at the Pacific Biological Station, Departure Bay, B.C., from 1929 to 1934. During the winter of 1934–35, financial assistance in the form of a Special Open Fellowship of the University of Toronto, was received, and the work carried on in the Department of Biology at the University of Toronto.

The writer wishes to express her appreciation of the assistance given her by Dr. E. M. Walker in his supervision of the work at the University of Toronto. She is also indebted to Dr. W. A. Clemens for his interest and suggestions during the progress of the experimental work, and would like to thank the members of the staff of the Pacific Biological Station for their helpful co-operation at all times.

References

1. Alcock, A. A catalogue of the Indian decapod Crustacea in the collection of the Indian museum. Part II. Anomura. Fasc. I, Indian Museum, Calcutta. 1905.
2. Bell, T. A history of British stalk-eyed Crustacea. London. 1853.
3. Benedict, J. E. A question concerning a British pagurid. Ann. Nat. Hist. 18 : 99-100. 1896.
4. Benedict, J. E. The anomuran collections made by the Fish Hawk Expedition to Porto Rico. Bull. U.S. Fish Comm. 20 : 131-148. 1900.
5. Berkeley, A. A. The post-embryonic development of the common pandalids of British Columbia. Contr. Can. Biol. 6 : 81-163. 1930.
6. Boas, J. E. V. Studier over Decapodernes Slaegtskabsforhold. Kgl. Danske Videnskab. Selskab, Skrifter, Naturvidenskab. math. Afdel. Ser. 6 : 1. 1880.
7. Bovard, J. F. and Osterid, H. L. Partial list of animals yielding embryological material at Puget Sound Biological Station. Puget Sound Biol. Sta. Pub. 2 : 127-137. 1918.
8. Borradaile, L. On the classification of the Thalassinidea. Ann. Mag. Nat. Hist. 12: 534-551. 1903.
9. Borradaile, L. On the classification and genealogy of the reptant Decapoda. XI. The fauna and geography of the Maldive and Laccadive Archipelagoes. Edited by J. Stanley Gardiner, Cambridge. 1906.
10. Borradaile, L. On the classification of the decapod Crustaceans. Ann. Mag. Nat. Hist. 19 : 457-486. 1907.
11. Bouvier, E-L. Crustaces decapods (macroures marcheurs) provenant des Campagnes des Yachts "Hirondelle" et "Princess Alice" (1885-1915). Res. Camp. Sci. Monaco. Facs. 50. 1917.
12. Calman, W. T. Crustacea. Lankester's treatise on zoology. London. 1909.
13. Calman, W. T. The life of Crustacea. London. 1911.
14. Cano, G. Sviluppo postembrionale della *Gebia*, *Axius*, *Callianassa*, e *Calliaxis*. Boll. soc. natural. Napoli, (1) : 5. 1891.
15. Garstang, W. The theory of recapitulation. J. Linnean Soc. Zool. 35 : 81-101. 1922.
16. Gurney, R. Decapod larvae. British Antarctic ("Terra Nova") Expedition, 1910. Zoology, 8 : (2). Crustacea, 9 : 37-202. 1924.
17. Gurney, R. Notes of some decapod Crustacea from the Red Sea. II. The larvae of *Upogebia savignyi* Strahl. Proc. Zool. Soc. London. Ser. B : 98-99. 1937.
18. Hart, J. F. L. Some decapods from the southeastern shores of Vancouver Island. Can. Field Naturalist, 54 : 101-109. 1930.
19. Hart, J. F. L. The larval development of British Columbia Brachyura. I. Xanthidae, Pinnotheridae (in part) and Grapsidae. Can. J. Research, 12 : 411-432. 1935.

20. HART, J. F. L. Culture methods for Brachyura and Anomura. The Collecting Net, 10 : 199-200. 1935.

21. HART, J. F. L. Culture methods for Brachyura and Anomura. Culture methods for invertebrate animals. 237-238. New York. 1937.

22. ISSEL, R. Ricerche intorno all biologia ed all morfologia dei Crostacei decapodi. Parte I. Studi sui Paguridi. Archivio Zoologica, 4 : 335-398. 1910.

23. LEBOUR, M. V. The larval stages of the Plymouth Brachyura. Proc. Zool. Soc. London, 473-560. 1928.

24. LEBOUR, M. V. The larval stages of *Caridion*, with a description of a new species, *C. steveni*. Proc. Zool. Soc. London, 181-194. 1930.

25. LEBOUR, M. V. Notes on the Plymouth species of *Spirontocaris* (Crustacea). Proc. Zool. Soc. London, 89-104. 1936.

26. MCGINITIE, G. E. The natural history of the mud-shrimp, *Upogebia pugettensis* (Dana). Ann. Mag. Nat. Hist. 6 : 36-44. 1930.

27. MARUKAWA, H. Biological and fishery research on Japanese king-crab, *Paralithodes camtschatica* (Tilesius). J. Imp. Fish. Expt. Sta. Tokyo, 4 : 123-152. (In English.) 1933.

28. MENON, M. K. The life histories of decapod Crustacea from Madras. Madras Gov. Museum, n.s. Nat. Hist. Sect. 3 : 1-45. 1933.

29. MILNE-EDWARDS, H. Histoire naturelle des Crustaces. 1834.

30. MÜLLER, F. Für Darwin. Leipzig. 1864.

31. NEEDLER, A. B. Larvae of some British Columbian Hippolytidae. Contr. Can. Biol. 8 : 239-242. 1933.

32. ORTMANN, A. Die Decapoden-Krebse des Strassburger Museums. 8 pts. Zool. Jahrb. Abth. Syst. 5-7. 1890-1891.

33. ORTMANN, A. Die Klassen und Ordungen der Arthropoden. Bd. 5, (2). Abth. Crustacea Malacostraca. Leipzig. 1901.

34. ORTON, J. H. On the mode of feeding of the hermit crab, *Eupagurus bernhardus* and some other decapods. J. Marine Biol. Assoc. 14 : 909-921. 1926-1927.

35. RATHBUN, M. J. The fossil stalk-eyed Crustacea of the Pacific slope of North America. U.S. Nat. Mus. Bull. 138 : 1-155. 1926.

36. RATHKE, H. Zur entwickelungsgeschichte der Dekapoden. Arch. naturgesch. 6 : 241-249. 1840.

37. RATHKE, H. Beiträge zur vergleichenden anatomie und physiologie. II. Zur entwickelungsgeschichte der Dekapoden. Neuste schr. naturforsch. ges. Danzig. 3 : 23-55. 1842.

38. SARS, G. O. *Nephrops, Calocaris, Gebia*. IX. Bidrag til Kundskaben om Decapodernes Forvandlinger. Arch. Math. Naturvidenskab. 1884.

39. SARS, G. O. *Lithodes, Eupagurus, Spiropagurus, Galathodes, Munida, Porcellana*. XIII. Arch. Math. Naturvidenskab. 1889.

40. STEVENS, B. A. Hermit crabs of Friday Harbor, Washington. Puget Sound Biol. Sta. Pub. 3 (68) : 273-309. 1925.

41. STEVENS, B. A. *Orthopagurus*, a new genus of Paguridae from the Pacific coast. Puget Sound Biol. Sta. Pub. 5 : 245-252. 1927.

42. STEVENS, B. A. Callianassidae from the west coast of North America. Puget Sound Biol. Sta. Pub. 6 : 315-369. 1928.

43. THOMPSON, J. V. Zoological researches and illustrations. I. Cork. 1828.

44. THOMPSON, J. V. On the metamorphoses of decapodous Crustacea. Zool. J. 5, (19) : 383-384. 1830-1831.

45. THOMPSON, M. T. The metamorphoses of the hermit crab. Proc. Boston Soc. Nat. Hist. 31 : 147-209. 1903.

46. WEBB, G. E. The development of the species of *Upogebia* from Plymouth Sound. J. Marine Biol Assoc. n.s. 12 : 81-135. 1919.

UB

V 15 10 OCT 37
UMI